UNIVERSITY OF TORONTO
3 1761 01578674 2

RECENT ADVANCES IN CYTOLOGY

RECENT ADVANCES IN PLANT GENETICS

By F. W. Sansome, Ph.D., F.L.S., F.R.S.E., and J. Philp, B.Sc., F.L.S.
55 Illustrations. 15*s*.

RECENT ADVANCES IN BOTANY

By E. C. Barton-Wright, M.Sc.
60 Illustrations. 12*s*. 6*d*.

Also by E. C. Barton-Wright :

RECENT ADVANCES IN PLANT PHYSIOLOGY

51 Illustrations. 12*s*. 6*d*.

A TEXT-BOOK OF BOTANY

By James Small, D.Sc., Ph.C., F.R.S. (Edin.). Second Edition. With over 1,350 Illustrations. 21*s*.

Also by Professor Small :

PRACTICAL BOTANY

35 Illustrations. 10*s*. 6*d*.

RECENT ADVANCES IN AGRICULTURAL PLANT BREEDING

By Dr. H. Hunter and Dr. H. M. Leake.
Ready Shortly.

J. & A. CHURCHILL

RECENT ADVANCES IN CYTOLOGY

By

Cyril Dean

C. D. DARLINGTON

D.Sc., Ph.D.

Cytologist, John Innes Horticultural Institution

With a Foreword by

J. B. S. HALDANE, M.A., F.R.S.

Head of Genetical Department, John Innes Horticultural Institution ;
Sir William Dunn Reader in Bio-Chemistry, University of Cambridge ;
Fullerian Professor of Physiology, Royal Institution

With 8 Plates, 109 Text-figures
and 66 Tables

279825
11. 11. 32

LONDON
J. & A. CHURCHILL
40 GLOUCESTER PLACE
PORTMAN SQUARE
1932

To

F. A. JANSSENS
1863–1924

W. C. F. NEWTON
1894–1927

KARL BELAR
1895–1931

Printed in Great Britain

FOREWORD

I AM fortunate in being allowed to write a foreword to this book. It should properly, I think, be termed a treatise on karyology, the study of the nucleus, rather than on cytology, of which karyology is a part. For no mention is made of extra-nuclear constituents of the cell except in their relation to the nucleus. In karyology it marks the beginning of a new epoch, the transition from an essentially descriptive to a largely deductive science. Perhaps the closest parallel may be found in the study of the "fixed" stars. The earlier investigators were concerned with technique and classification. Methods of microscopy and telescopy were improved. Organisms were classified according to the number, structure and behaviour of their chromosomes, stars according to their luminosities, masses and spectra. The work of Emden, Eddington, Saha, Jeans and Milne has made astrophysics a largely deductive science. Darlington and a few others are doing the same for karyology.

The average cytologist is primarily an observer, and unaccustomed to long chains of deductive reasoning. He will find this book extremely difficult. Unfortunately it is indispensable. For Dr. Darlington's deductive principles stand the test of practical application. As his colleague I can testify that he has investigated an apparently most heterogeneous series of plants with a very clear idea of what he was looking for in each case, and that on more than half of these occasions he found it. I observed a similar series of phenomena during some years when I occupied the next room to Professor Milne.

The analogy with astrophysics can be carried still further. The study of inorganic evolution can be followed to advantage in the fixed stars because they are extraordinarily like one another. But the student of organic evolution who confines himself to macroscopic morphology is hampered by the extreme diversity of his material. It is difficult to be an expert at once on mammalian teeth, ammonite sutures and pteridosperm vascular bundles. But the chromosomes are not only astonishingly similar in all organisms, but are mainly responsible for the diversities of teeth and xylem. And their study immediately discloses a whole set of new evolutionary principles which were hidden from the macroscopic morphologist.

It is improbable that all the conclusions of Dr. Darlington's last chapter are correct. Probably comparative biochemistry will effect as great changes in our view of evolution as comparative morphology. Nevertheless I am convinced that the last chapter is a prolegomenon to every future theory of evolution. I do not pretend that I have yet fully digested it. Until I do so my opinions on evolution will be of somewhat restricted value. But I am already clear that no serious student of evolutionary biology can conceivably avoid reading it.

J. B. S. HALDANE.

PREFACE

THE present work attempts to describe one aspect of cytology, the study of the nucleus and the chromosomes in plants and animals. It consists of three elements: an introduction for the student who is a beginner, a résumé for the research worker who requires classified observations, and a theoretical treatise, in which my own views are developed, for the general biologist.

To the student I would say that of course he cannot learn the subject from "bookish theoric," but he will find the first eight chapters a guide to his early observations. To the research worker I would say that here he has a great many hypotheses presented to him which, even if incorrect, may serve to suggest some new directions of enquiry. To the general biologist I would point out that here is a study resting on its own postulates and using its own technique, a study which provides an independent tool for the investigation of heredity, variation and evolution. It is related in every part to the sister-science of genetics, but is no longer a handmaiden of genetics. The chromosomes are shown in their relation to the organism as a whole, not merely as bearers of hereditary characters. Finally, in no branch of biology will he find the subject-matter of the whole science presented in closer unity.

It is four years since Belar wrote his *Cytologische Grundlagen*—the last attempt to give a general account of chromosome behaviour. During this time an important change has come over the study. Its methods have come to be quantitative and analytic instead of merely morphological. It has therefore been possible to arrive at new interpretations of behaviour and new generalisations of cause and effect. These new conclusions have to be applied to the old observations; they also have to be applied to many new ones. I have taken the liberty of attempting these tasks, of trying to assimilate the old observations to the new theories. "I can promise to be candid but not impartial." I hope the authors will forgive me.

Previous descriptions of the properties of the chromosomes have consisted in a detailed morphological account combined with demonstrations of the explanatory value of the chromosome theory of heredity. The importance of the chromosomes as determining the hereditary functions has placed them outside the ordinary field of evolutionary enquiry. They have been considered as the very fount and origin of adaptive change and therefore not themselves capable of adaptation. Now they can be shown to be subject to the genetical variation which they themselves, by changes in their parts, determine. In this way it becomes possible to consider the chromosomes to a great extent like other structures in their relation to the organism as a whole, and to attempt a causal explanation of the whole range of chromosome phenomena in genetical terms. We have a coherent system of enquiry into the hereditary mechanism which is less dependent on the technique and secondary assumptions of breeding work, simply because it is directly built, as all biological studies must be, on the primary genetic postulates.

It is therefore especially important in approaching this study to enunciate these postulates and use them consistently. This has been attempted as far as possible. Let it be particularly noted that such terms as "gene," "hybridity" and "homology" should not be used as an abracadabra for the solution of all recalcitrant difficulties. They are of the utmost value when kept close to their empirical basis, but when loosely defined or loosely applied they can be used, and often are used, to obscure the issue and misdirect the enquiry. I have taken particular pains to define all such terms.

With regard to observations there is now less room for controversy than heretofore. At the same time it must be remembered that the distinction between fact and hypothesis made in everyday life becomes too naïve when applied to the data of a new study. Every "fact" implies a hypothesis. It will be seen that on several occasions where "fact" and "hypothesis" have recently come into conflict in cytology, hypothesis has won the day simply because the alleged facts have differed from the hypotheses in being derived from concealed (and erroneous) assumptions instead of from open (and valid) ones.

This does not mean that the distinction between fact and theory is useless. The distinction is useful so long as we remember that it is arbitrary. It is often passed over in a curious way. Many so-called theories of recent years are mere corollaries directly deduced from simple and accepted generalisations and they involve no new assumption whatever. Such truisms are valuable but are misnamed. Again the arguments for many hypotheses have been expressed teleologically (for example in regard to the conditions of meiosis and the origin of polyploidy). These may be valuable so long as it is recognised that the introduction of the idea of purpose is a logical ellipsis and not, as it suggests, a definitive explanation.

As the logical coherence of the study increases, the difficulty of orderly description increases too. Every phenomenon can be described in relation to one or other of its causes or results. The subject-matter of chromosome cytology is derived from a study of two forms of nuclear division, mitosis and meiosis. Observations may be considered in relation to the one of these sources from which they are derived or in relation to the genetic or environmental conditions determining them or determined by them. Observations of meiosis may be taken to show the mechanism of genetic crossing-over and segregation. They may be taken to show meiosis as an abnormality of mitosis and as the origin of sexual reproduction. Again they may be taken to show the forces the chromosomes exert on one another under special conditions, and thus may throw light on the mechanics of chromosome behaviour and of cell-division. Finally they may be taken to show, by the comparison of hybrids with pure forms, how the chromosomes act when their behaviour is governed by their reaction not only with genotype and environment but also with one another. Observations from all these points of view I have had to consider separately, but in order to show their relationship with one another and with the properties of the organism-as-a-whole they have been considered finally in their bearing on the central problem of evolution. This involves hypotheses, some of them of a speculative kind. But we must remember, as Huxley said, that those who refuse to go beyond the fact rarely get as far as the fact. We need to see a little ahead of us, and a theory may save us from stumbling in the dark. If some of the hypotheses here advanced prove to be will-o'-the-wisps, others I hope will lead to tangible discoveries.

I am particularly indebted to Professor J. B. S. Haldane both for encouragement and for criticism he has given me in the preparation of this book and in earlier work. I am also indebted to Dr. Nellie Carter, of the East London College, and to my colleagues, Miss D. M. Cayley and Miss Irma Andersson-Kottö, for advice on Algæ, Fungi and ferns. I have to thank Miss Hilda Schafer for bibliographical work and the translation of Russian papers, and my colleagues, Miss A. E. Gairdner, Mrs. E. R. Sansome, Mr. W. J. C. Lawrence, Mr. A. A. Moffett, Mr. S. O. S. Dark and Mr. K. Mather, for the use of their unpublished illustrations ; also the many authors mentioned in the text for their kindness in allowing me to reproduce photographs and figures, some of them unpublished.

C. D. DARLINGTON.

XI

TABLE OF CONTENTS

CHAPTER I

INTRODUCTION

PAGE

1. **The Nucleus, the Cell and the Organism** 1
   (i) The Problem ; (ii) Structure ; (iii) Differentiation.

2. **Reproduction** 4
   (i) Asexual Reproduction ; (ii) Sexual Reproduction ; (iii) Sexual Differentiation : The Gametes.

3. **Heredity** 10
   (i) Genotype and Environment ; (ii) Conditions of Sexual Differentiation.

CHAPTER II

MITOSIS. THE CONSTANCY OF THE CHROMOSOMES

1. **The Resting Nucleus** 16

2. **The Behaviour of the Chromosomes** 19
   (i) Introduction ; (ii) Prophase ; (iii) Metaphase : the Spindle ; (iv) Anaphase ; (v) Telophase ; (vi) Duration of Mitosis.

3. **Abnormal Forms of Mitosis** 28

4. **The Structure of Chromosomes** 30
   (i) At Prophase : Spiral Structure ; (ii) At Metaphase and Anaphase : Constrictions and Trabants ; (iii) In the Resting Stage : The Theory of Permanence ; (iv) When do the Chromosomes Divide ?

CHAPTER III

MITOSIS. THE VARIATION OF THE CHROMOSOMES

PAGE

1. **The Subordination of the Chromosomes to the Genotype** . 50
   (i) The Chromosome Constants at Mitosis ; (ii) Instances of Genotypic Control ; (iii) Conclusion.

2. **Numerical Variation of the Chromosomes** 59
   (i) Classification of Changes ; (ii) Polyploidy ; (iii) Polysomy.

3. **Structural Variation of the Chromosomes** 67
   (i) Classification ; (ii) Time, Place, and Action of Structural Change.

4. **Comparative Morphology of the Chromosome Complement** . 77
   (i) Specific ; (ii) General.

CHAPTER IV

MEIOSIS IN DIPLOIDS AND POLYPLOIDS

1. **Introduction** 87

2. **Outline of Meiosis** 88

3. **Meiosis in Diploids** 91
   (i) The Pairing of the Chromosomes ; (ii) The Separation of the Chromosomes and the Origin of Chiasmata ; (iii) Diakinesis ; (iv) The Movement of Chiasmata ; (v) Metaphase : the Structure of the Bivalent Chromosomes ; (vi) Anaphase : the Separation of the Chromatids ; (vii) Interphase ; (viii) The Second Division.

4. **Meiosis in Polyploids** 114
   (i) Prophase ; (ii) Metaphase : The Limits of Chromosome Association ; (iii) The Two Divisions.

5. **Conclusion : The Principles of Chromosome Pairing** . . 126

CHAPTER V

MEIOSIS IN STRUCTURAL HYBRIDS

PAGE
1. **Definition and Classification of Hybrids** 128
2. **Meiosis in Structural Hybrids** 132
   (i) Method of Analysis; (ii) Fragmentation and Fusion Heterozygotes; (iii) Translocation Heterozygotes; (iv) Reduplication Heterozygotes; (v) Interchange Heterozygotes; (vi) Polyploid Interchange Heterozygotes; (vii) Unequal Pairs of Chromosomes.

CHAPTER VI

MEIOSIS IN UNDEFINED HYBRIDS

1. **The Conditions of Chromosome Pairing** 156
2. **Chromosome Pairing in Undefined Hybrids** 160
3. **The Behaviour of Unpaired Chromosomes** 165

CHAPTER VII

THE BEHAVIOUR OF POLYPLOIDS

1. **The Origin of Polyploids in Experiment** 169
2. **Polyploid Species** 181
3. **Differential Affinity: Autosyndesis** 182
4. **Classification of Polyploid Species** 196

CHAPTER VIII

THE EVOLUTION OF POLYPLOIDS

1. **The Development of the Polyploid Species** 204
   (i) Introduction; (ii) Variation in Cell Size; (iii) Polyploidy within the Species.
2. **The Inference of Polyploidy** 212
   (i) Statistical Evidence; (ii) New Polyploid Species; (iii) Somatic and Secondary Pairing; (iv) Secondary Polyploidy.

CHAPTER IX

THE CHROMOSOMES IN HEREDITY. PART I

PAGE

1. **The Chromosome Theory of Heredity** 227

2. **The Qualitative Differentiation of the Chromosomes** . . 229

   (i) Evidence from Meiosis; (ii) Balance—(*a*) Monosomics; (*b*) The Progeny of Triploids; (*c*) Secondary Balance.

3. **The Gene in Relation to Mutation and Balance** . . . 244

4. **Segregation** 247

CHAPTER X

THE CHROMOSOMES IN HEREDITY. PART II

CROSSING-OVER

1. **The Theory of Crossing-Over** 250

   (i) Introduction; (ii) The Genetic Theory; (iii) The Cytological Theory.

2. **Cytological Proof of Crossing-Over** 260

   (i) Proof of whether Crossing-over Occurs; (ii) Proof of When and Where Crossing-over Occurs—(*a*) On Developmental Assumptions; (*b*) On Physiological Assumptions.

3. **Cytological Evidence of Crossing-Over** 270

   (i) From Anaphase Separation of Chromosomes; (ii) From Prophase Interlocking of Chromosomes; (iii) From the Segregation of Unequal Bivalents.

4. **Evidence by Parallel Inference from Chiasmata and Crossing-Over** 277

   (i) In Diploids (General); (ii) In Polyploids; (iii) In Structural Hybrids; (iv) Conditions of Variation; (v) Linear Distribution—(*a*) In Relation to one Another (Interference); (*b*) In Relation to Position (Map-Distance).

5. **Evidence of How Crossing-Over Occurs** 288

CHAPTER XI

THE THEORY OF MEIOSIS

PAGE
1. **Historical Sketch** 294
2. **Relation of Meiosis to Mitosis** 300
   (i) The Essential Characteristics of Mitosis ; (ii) The Essential Characteristics of Meiosis—The Resting Stage ; Leptotene-Zygotene ; Pachytene-Diplotene ; Diakinesis ; Metaphase-Anaphase ; The Second Division.
3. **The Precocity Theory** 306

CHAPTER XII

THE MECHANICS OF CHROMOSOME BEHAVIOUR

1. **The Classification of Chiasmata** 309
2. **Terminalisation** 311
   (i) General Character of the Change ; (ii) The Origin of Terminal Chiasmata ; (iii) Conditions Affecting Terminalisation ; (iv) The Forces Affecting Chiasma Movements ; (v) The Relation of Terminalisation to other Phenomena.
3. **The Theory of the Terminal Chiasma** 328
   (i) The Problem ; (ii) The Method ; (iii) Forces at Prophase ; (iv) Forces at Metaphase ; (v) Forces at Anaphase ; (vi) Classification of Forces.
4. **The Analysis of Chromosome Movement** 335

CHAPTER XIII

ABNORMALITIES OF MEIOSIS

1. **Genetically Determined Failure of Pairing** 344
   (i) Classification ; (ii) Failure through Lack of Precocity of the Division ; (iii) Failure through Precocity of particular Chromosomes ; (iv) Failure through Lack of Chiasmata ; (v) Exceptional Failure in Normal Forms.

PAGE

2. Irregularities of Meiosis 357

(i) Classification ; (ii) Irregularities due to Failure of Pairing ; (iii) Irregularities due to Failure of the Spindle Mechanism ; (iv) Meiosis in Haploids ; (v) Conclusions.

3. The Imitation of Meiosis : Polymitosis 366

4. Abnormal Forms of Meiosis 368

(i) Introduction ; (ii) In *Rosa canina* ; (iii) In the Coccidæ.

CHAPTER XIV

PERMANENT DIPLOID HYBRIDS

1. Introduction 376

2. Sex Heterozygotes 378

(i) Types of Sex Chromosomes ; (ii) Pairing of Sex Chromosomes ; (iii) Segregation of Sex Chromosomes ; (iv) Note on Genetics of Sex Determination ; (v) The Differentiation of the Sex Chromosomes ; (vi) Conclusions.

3. Complex Heterozygotes 398

(i) Introduction ; (ii) Inheritance in *Œnothera* ; (iii) Chromosome Behaviour in *Œnothera* ; (iv) Mutations.

CHAPTER XV

APOMIXIS

1. Definition and Classification 416

2. Apomixis in Relation to the Life Cycle 417

(i) Higher Animals (Metazoa)—(*a*) Diploid Parthenogenesis ; (*b*) Haploid Parthenogenesis ; (ii) Ferns (Pteridophyta)—(*a*) Diploid Parthenogenesis ; (*b*) Apospory ; (*c*) Apogamy ; (*d*) Apospory with Apogamy ; (iii) Flowering Plants (Angiospermæ)—(*a*) Diploid Parthenogenesis ; (*b*) Apogamy ; (*c*) Apospory ; (*d*) Apospory with Apogamy ; (iv) Lower Organisms (Thallophyta and Protista).

PAGE
3. **Non-Recurrent Apomixis** 424
(i) Parthenogenesis ; (ii) Regeneration and Apospory.

4. **Apomixis in Relation to Meiosis** 430
(i) Meiosis in Functional Cells ; (ii) Meiosis in Non-Functional Cells ; (iii) Meiosis in Haploids ; (iv) Meiosis in Cyclical Parthenogenesis.

5. **The Origin of Apomixis in Experiment** 441
(i) Pseudogamy ; (ii) Injury ; (iii) Mutation ; (iv) Hybridisation ; (v) The Evidence of Chromosome Numbers.

CHAPTER XVI

THE EVOLUTION OF GENETIC SYSTEMS

1. **Premises** 448

2. **The Chromosomes and Mitosis** 450
(i) The Naked Gene : reproduction and mutation ; (ii) Aggregation and Differentiation ; (iii) Construction of Chromosomes ; (iv) Spindle Mechanism ; (v) Structural Change.

3. **The Origin of the Sexual Cycle** 454
(i) Fusion or Addition : Diploidy ; (ii) Origin of Meiosis : Advantages ; (iii) Restriction of Meiosis in Time and Space ; (iv) Development of the Meiotic Spindle Mechanism ; (v) Modifications of Chromosome Behaviour.

4. **The Development of the Sexual Cycle** 460
(i) Origin of Sexual Differentiation ; (ii) Cytological Development of Differentiation ; (iii) Changes in Sexual Differentiation ; (iv) The Haplo-Diploid System.

5. **The Stabilisation of Hybridity** 469
(i) The Development of Apomixis ; (ii) Ring-Formation : The Complex Heterozygote ; (iii) Polyploidy.

6. **Conclusions** 478
(i) The Sources of Variation ; (ii) The Nature of Species ; (iii) The Principles of Evolutionary Change.

PAGE

Appendix I Cytological Interpretation 486

" II Recent Improvements in Technique . . . 491

" III Glossary 493

" IV Bibliography 503

Index 543

RECENT ADVANCES IN CYTOLOGY

CHAPTER I

INTRODUCTION

The Cell and the Nucleus—Differentiation—Reproduction—Asexual and Sexual—Haploid and Diploid Phases—Sexual Differentiation—Genotype and Environment—Their Bearing on Chromosome Behaviour—And on Sexual Differentiation.

> quippe, ubi non essent genitalia corpora cuique,
> qui posset mater rebus consistere certa ? [1]
> LUCRETIUS, *De Rerum Natura*, I, 167—168.

1. THE NUCLEUS, THE CELL AND THE ORGANISM

(i) **The Problem.** The object of the present work is to describe the bodies responsible for heredity, to show how they live, move and have their being. We now know that Lucretius was right ; there are such bodies. But before considering them we must see how organisms are constructed, how they reproduce and how heredity expresses itself. Then we can examine the *genitalia corpora* and better understand their relations with heredity.

(ii) **Structure.** The living organism contains certain materials which for various reasons are held to be non-living. Such, for example, are the skeletal structures of plants and animals, consisting largely of cellulose, calcium carbonate or chitin, their storage products, such as starch, fats and glycogen, and their fluid contents, such as cell sap and blood plasma. The rest of the plant or animal body is described for convenience as the living substance or "protoplasm." Various non-living substances, such as water, can be separated from it without altering its essential character. Protoplasm is a structural unit, not a chemical entity.

---

[1] For, if each organism had not its own begetting bodies, how could we with certainty assign to each its mother ?

In certain organisms no differences of structure have yet been detected between different parts of the protoplasm. In most bacteria this is perhaps due to their small size. In the Cyanophyceæ and larger bacteria, differences are still being sought for. Elsewhere it is always possible to distinguish between a small dense *nucleus* and the rest of the living substance, which is called cytoplasm. In the cytoplasm other bodies can be very generally made out ; they are known generically as chondriosomes and plastids. They are not as yet universally recognised, and their relation, with one another in different groups of organisms are not always clear. The nucleus, on the other hand, can be seen in all stages of development. It is always carried by the germ cells of both parents in sexual reproduction and is the only structure of which this is known. It is recognised customarily by its characteristic method of propagation. All nuclei arise by division of a pre-existing nucleus into two. To do this, the mother-nucleus resolves itself into a number of double bodies, the chromosomes, two structurally equivalent products, and all the descendants of a nucleus derived in this way have the same complement of chromosomes. This process is known as *mitosis*.

All organisms may be said to arise from bodies of protoplasm with single nuclei. Each of these is described as a single *cell*. In the lowest organisms with nuclei, the Protista, growth of this cell is followed by its division, together with that of its nucleus, by mitosis, and the separation of the daughter cells. The organism thus remains unicellular. The simplicity of its organisation is not always associated with simplicity of structure within the cell. Indeed, while the Protista necessarily embrace the simplest organisms they also include those with the most complex development within the cell. This range of cellular evolution is matched by a range of form of the nucleus and of its methods of division greater than that found in all the higher animals and plants (*v*. Ch. II), as is indeed appropriate in what must necessarily be the oldest group of organisms. In many of the lower organisms (Myxomycetes, Phycomycetes, some Chlorophyceæ) division of the nucleus is not accompanied by division of the cell, that is of the whole organism, which in consequence comes to contain many nuclei; it is multinucleate. Elsewhere, division of the cell into two compartments takes place at the same time as division of the nucleus. The daughter cells may be separated by non-living secretions of the cell with a connective or cementing function, or by differentiated parts of their own cytoplasm. The organism developing in this way is said to be multicellular. It reproduces by the separation of either single cells or groups of cells from the main body. Both unicellular and multicellular organisms may pass through a multinucleate stage of development, *e.g.*, at spore formation in many Protista, in the germ tubes of the Basidiomycetes and in the pollen tubes of flowering plants.

Apart from these special conditions the term "cell" is a convenient designation for a separate body of protoplasm containing a single nucleus.

(iii) **Differentiation.** Certain cells may reproduce themselves without change indefinitely under constant conditions. This is true of many Protista, as well as of many young cells of the higher animals in tissue culture. Change of conditions leads to a change in appearance or behaviour affecting the whole life of the organism, such as encystation in the Protista. But even under constant conditions the products of cell division are usually dissimilar from the parent cell. In the Protista in which a series of different forms occur in regular or irregular sequence, making up the "life cycle," the daughter cells are usually like one another but unlike the parent cell. This may be spoken of as differentiation-in-time. In multicellular organisms one of the daughter cells is usually unlike either the parent or its sister; in this way the organism comes to consist of many cells of different forms and properties. This may be spoken of as differentiation-in-space. With higher organisation (both in the Protista and elsewhere) external conditions have less and less to do with the direction of differentiation of particular cells although they continue to modify its rate and consequently affect the result in detail. We may say that, in general, the greater the internal capacity for differentiation the less the special reaction to external changes.

2. REPRODUCTION

(i) **Asexual Reproduction.** Growth and reproduction equally depend on increase in size and in organisms having a differentiation of their substance into nucleus and cytoplasm, both are necessarily related to nuclear division.

In the unicellular Protista, in which each individual has a single nucleus, or a pair of complementary nuclei, division of the nucleus entails division of the whole organism: mitosis is an act of reproduction. In multicellular organisms, division is merely a concomitant of growth. In these under suitable conditions such growth is indefinite. The conditions occur in many species of Protista, which reproduce indefinitely without sexual process. They are found in the higher plants where vegetative propagation can be carried on without limit, either naturally in the formation of bulbs, runners, viviparous shoots or apomictic seeds (to which special consideration will be given later) or artificially in propagation by cuttings and layers, buds and grafts. Many species of plants and animals depend for their preservation on these purely asexual or "vegetative" means of propagation. This is usually associated with great uniformity within the species, which in plants may be described as "clones."

Reproduction by mitosis alone can therefore continue indefinitely. Cases where it has failed to do so and where vitality can then be restored by sexual reproduction are due to special adaptation to conditions of sexual reproduction.

(ii) **Sexual Reproduction.** Sexual reproduction is known in all groups of living organisms with nuclei. In the Flagellata it has only been established in three genera (*cf.* M. Robertson, 1929) and in the Protista as a whole it is difficult as yet to estimate its importance. Elsewhere, however, whether normally or in some modification, it is an essential part of the life cycle of nearly all species.

Sexual reproduction consists superficially in the formation and separation from the rest of the organism of single cells, the germ-cells or *gametes* (constituted by the whole organism, in the Protista, and by a specialised part of it, in the higher plants and animals) and their subsequent fusion in pairs to give new cells, known as *zygotes*.

Its essential genetic characteristics are two. The first was seen by Oscar Hertwig (in 1875) to consist in the fusion of the nuclei of the two gametes. Since they carry the same number of chromosomes the product has the double or " diploid " number. This is *fertilisation.* The second was predicted by Weismann (in 1887). It consists in the compensating process of reduction or *meiosis.* In a " mother-cell " two nuclear divisions follow one another rapidly while the chromosomes only divide once, so that four nuclei are formed, to each of which a halved or " haploid " number of chromosomes is distributed.

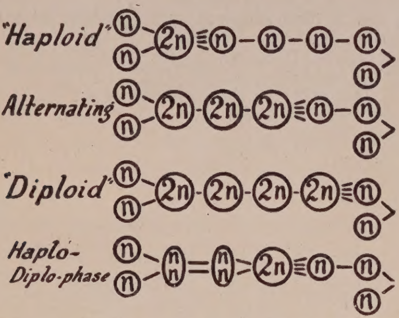


FIG. 1.—Diagram to show the relation of meiosis and fertilisation to the different types of life cycle. Converging lines, fertilisation (in two stages with diplophase) ; diverging lines, meiosis.

The recurrence of fertilisation and meiosis gives two types of nuclei in each sexually reproducing species, the " diploid " or double nucleus of the zygote and the " haploid " or halved nucleus of the gamete. Either or both of these may, in different species, continue to multiply by mitotic divisions, giving a number of unicellular organisms or one multicellular one, so that we have three types of reproductive cycle, according to the importance of the diploid or haploid phase, as follows :

(*a*) Meiosis immediately follows fertilisation (" zygotic reduction "). The organism is then purely haploid, apart from the zygote (Fig. 1).

(*b*) Fertilisation immediately follows meiosis (" gametic reduction"). The organism is then purely diploid, apart from the gametes (Fig. 1).

(*c*) A mitotic generation is intercalated after each process. There is then an alternation of haploid and diploid generations. The single cell from which the haploid generation is derived is called a "spore." The spore mother-cell of the diploid "sporophyte" produces haploid spores from which the haploid "gametophytes," known as "prothallia" in the pteridophyta, are developed, and these bear the haploid gametes which fuse and give the new sporophyte. The gametophyte and sporophyte may be indistinguishable from one another morphologically (as in most Rhodophyceæ) save in the production of sexually differentiated germ-cells by the gametophyte and of non-motile spores by the sporophyte. Usually, however, the two generations are sharply distinct and the less important generation (as in the Bryophyta and

TABLE 1

Variation in the Haploid and Diploid Generations

	Purely Haploid, "Zygotic Reduction."	Predominantly Haploid (phases dissimilar).	Equally Haploid and Diploid (phases similar).	Predominantly Diploid (phases dissimilar).	Purely Diploid, "Gametic Reduction."
PROTISTA.	Flagellata (some)[1] Sporozoa-Coccidia. (*e.g.*, *Aggregata* Dobell, 1925). Sporozoa-Gregarina (some).	—	—	—	Rhizopoda (some, *e.g.*, *Actinophrys*, Belar, 1924).[1] Ciliata (*e.g.*, *Paramœcium*, Jennings, 1920). Sporozoa-Gregarina (some).[3]
PLANTS.	Charophyta. Chlorophyceæ (most). Phycomycetes. Ascomycetes.[4] Basidiomycetes.[4]	Bryophyta.[2]	Chlorophyceæ (*e.g.*, *Cladophora*, spp., Schussnig, 1930, 1931). Rhodophyceæ (most). Phæophyceæ (most).	Phæophyceæ (*e.g.*, *Laminaria*). Myxomycetes (probably). Pteridophyta. Phanerogama.[2]	Chlorophyceæ (*e.g.*, *Cladophora*, spp., Higgins, 1930). Phæophyceæ (*e.g.*, *Fucus*).
ANIMALS.					All Metazoa.[5]

[1] Most are non-sexual.
[2] Subordinate phase parasitic on predominant phase.
[3] Some have one mitosis in the haploid phase.
[4] *v. Infra.*
[5] Except those with haplo-diploid sex-differentiation.

in the flowering plants) may be parasitic on the more important one. The following table classifies the main groups of animals and plants in this respect (*cf.* Belar, 1926 *b*; M. Robertson, 1929; Naville, 1931, for Protista; Correns, 1928, for Phanerogama; Hartmann, 1929, *a* and *b*, for lower plants; Witschi, 1929, for Metazoa).

(iii) Sexual Differentiation : The Gametes. Sexual differentiation consists in the production by the species of two kinds of germ-cells which are complementary. It is determined by the same kinds of conditions as all other differentiation. But it has such special importance in reproduction and in the evolution of particular genetic mechanisms that it requires special consideration.

Sexual differentiation is not found in the Flagellata, Phycomycetes or in many Chlorophyceæ, and it is negligible in the Rhizopoda, Gregarina (Sporozoa) and in the Basidiomycetes and other Fungi.

In all the higher organisms and in many Algæ and Protozoa there is a differentiation between a small, active or motile *male* cell and a large, inactive or non-motile *female* cell, usually charged with nutritive material and having a larger nucleus.

When the male gamete arises at meiosis, like the spore, where there is a haploid generation, the cytoplasm of its mother cell is equally divided among the four daughter cells (except in certain Diptera, *cf.* Metz). The female gamete arises (except in certain Mollusca and Turbellaria) by the suppression of all but one of the products of meiosis. This one becomes the egg nucleus, while the other products are extruded as the "polar bodies," which at once degenerate. Where a short haploid generation occurs (reduced and specialised for the production of the female germ-cells, as in *Lycopodium* and the higher plants) an intermediate condition is found. The four potential spores are almost equal; the gametophyte may then develop from one (*cf.* *Œnothera*, Ch. XIV), or from the collaboration of all four.

It is of particular importance in studying the mechanism and material basis of heredity to examine the male gamete—sperm, "antherozoid" or "generative nucleus" of the pollen grain. The female gamete is usually an over-developed cell, the male an under-developed one; that is to say, its constituents are reduced, and by studying their reduction we can see what is essential, and what unessential, in carrying the contribution of one parent in heredity.

Its development (*v.* Belar, 1928 *b*) shows that the simplest type of spermatozoon in the higher animals (*e.g.*, *Stenobothrus*) consists of four constituents: (i) Nucleus, making the "head" of the sperm; it is dense and stains deeply like the mitotic chromosomes. (ii) Centrosome, a cytoplasmic body, lying at the base of the nucleus, forming the "middle-piece" and often divided; from it develops the axial filament of the "flagellum" or tail. (iii) Mitochondria, cytoplasmic bodies making the sheath of the axial filament. (iv) Undifferentiated cytoplasm making a thin coat over the head and flagellum—part of the cytoplasm of the parent cell having often been rejected. (*Cf.* Bowen, 1924; Schrader, 1929.)

Sharp (1920, *et al.*) has shown the development of the male gamete, the "spermatozoid," in the Pteridophyta to follow the same course. It is possible to trace the origin of the spermatozoid from its antecedents: the material of the nucleus and the "blepharoplast," which corresponds to the centrosome and the middle-piece of the animal spermatozoon; it, also, is concerned with the development of cilia on the coat of the spermatozoid. The cytoplasm of the spermatid is left behind by the ripe gamete. In the flowering plants it is possible to show genetically and cytologically that in some species plastids are carried into the egg cell by the pollen tube, in others nothing but the nucleus passes from the male parent in fertilisation.

As a constituent of the male gamete the nucleus alone is constant in its contribution. All functional spermatozoa contain a nucleus which can be traced to one of the four bodies of chromosomes separated at meiosis. In certain organisms such as the flat-worm *Ancyracanthus* (Mulsow, 1912) and *Filaria* (Meves, 1915) the chromosomes can be counted as discrete bodies in the live and ripe sperms. The non-nuclear constituents, on the other hand, are variable in the proportion of their contribution. The same is true of the antherozoids of the lower plants. The centrosome, the only other permanent structure constantly carried by the sperm, is actually the one which is lost by the egg and transmitted on the male side only.

Both sperm and pollen grains are formed on occasion, particularly in hybrids with irregular meiosis, with a disorganised or incomplete nucleus or with a multiple nucleus. Spermatozoa with either too little (" oligopyrene " or " apyrene "), or too much, nucleus may develop the external apparatus of a sperm, or even function to give normal progeny. Kuhn (1929 *b*) found that sperms lacking certain chromosomes (the *X* and *Y*) functioned in fertilisation in *Drosophila*.

When pollen grains have too little nucleus, on account of their more complicated vegetative life, they never produce functional gametes or even develop as far as their vegetative division (*cf.* Ch. IX). When grains with too much nucleus function, they are of great importance in connection with the origin of polyploids and unbalanced forms (Chs. VII, IX, and XII).

The fusion of the nuclei in fertilisation usually takes place directly, but the process shows great variation. The two bodies of chromosomes may first unite at the mitosis which begins immediately before the nuclei meet (*e.g.*, *Ascaris*).

Two special types of fertilisation require consideration. In some fungi, fusion of nuclei does not immediately follow the fusion of their cells. In the Basidiomycetes the haploid spore develops into a mycelium containing haploid nuclei. The mycelium is at first multinucleate, but later cell-walls are formed so that each cell contains one haploid nucleus ; this is the " haplophase." Pairs of cells then fuse, derived from the same mycelium in " homothallic " species or from different mycelia in " heterothallic " species. But their nuclei do not fuse ; they exist and divide at each cell division side by side throughout the " diplophase." Eventually these " conjugate nuclei " fuse in the reproductive organ, the basidium, and the next division is meiosis which gives the four haploid spores. Thus, while the *cells* are diploid in the diplophase, the *nuclei* are haploid. Similar conditions are found in the higher Ascomycetes. The significance of this remarkable behaviour will be considered later (Fig. 1, *cf.* Ch. XVI).

In the flowering plants one kind of gametophyte, the pollen grain or microspore, produces the male gamete, its "generative nucleus," after undergoing two haploid mitoses, while another, the embryo-sac cell or megaspore, produces the female gamete, usually after three mitoses, together with seven other nuclei. Fertilisation is a double process, as shown by Navashin and Guignard in 1899 (*cf.* Stenar, 1927; Jørgensen, 1928; Dahlgren, 1927, 1930; Gerassimowa, 1932). The male gamete migrates through the cytoplasm of pollen-tube and embryo-sac and fuses with the egg nucleus. A second, sister, generative nucleus fuses with the product of fusion of two other nuclei in the embryo-sac to give the "triple fusion-nucleus" from which the nutritive endosperm develops, a new "triploid" organism with three nuclear complements, and independent of its sister embryo.

The female gametophyte, or embryo-sac, and the two embryos derived from it, although morphologically mere organs of the parent sporophyte, are genetically three distinct individuals. Since the endosperm is preponderantly maternal in origin (as shown cytologically by its origin and genetically by the properties it inherits) and its development is essential to the development of the embryo, for which it provides nutritive material, it follows that differences in seed production in reciprocal crosses between species, such as are frequently observed in the angiosperms, may be referred to the different relationships between embryo and endosperm (*cf.* Thompson, 1930; Watkins, 1932).

The new individual always arises from the fusion of the two germ-cells, and no others contribute normally. But it has been possible to show genetically that two fertilisations may take place side by side and the products join together to give a mosaic individual (Stern and Sekiguti, 1931, in *Drosophila*). In such a case probably another cell, the second polar body, functions as an auxiliary egg-cell. It is possible also that two pollen grains may function in fertilising the same egg-cell, both fusing with its nucleus, to give a triploid individual (Ishikawa, 1918, on *Œnothera*).

3. HEREDITY

(i) Genotype and Environment. Heredity is the property that organisms have of reproducing their like. It must be supposed, deterministically, that organisms carry something that they give to their offspring, and that this " something " determines the likeness. Under the simplest conditions, in the asexual reproduction of a clone or the sexual reproduction of an inbred race, it is always found that the likeness is imperfect ; further, the lack of likeness is not inherited, but is evidently due to the effect of different external conditions on the organism. This principle was first clearly recognised by Louis de Vilmorin. It was expressed by Weismann in the notion that the likeness was due to the constant properties of the *germ-plasm*, which was handed down unchanged from generation to generation. Finally, it was developed by Johannsen (1911, *et al.*) into the notion that the properties of an individual were the product of the reaction of its *genotype*, or type of germ-plasm, and the environment. On this notion genetical theory is built.

" Environment " requires a word of explanation. A fern may abnormally produce a prothallium vegetatively, and although the two must be supposed to have the same genotype their growth is entirely different. The reason is that although the two are separate individuals their development is conditioned by the circumstances of their origin, and the difference between them is simply a form of differentiation, the method of which is, like all other properties, a product of the genotype-environment reaction. So also with the various kinds of life cycle in the Protista : these are in different degrees subject to the variation in external conditions, but the different degrees of this subordination are to be considered a property of the genotype. Thus the visible properties of the organism (its phenotype) are the product of the reaction of its genotype with its environment. Further—and this is most important in the present study of cytology—differences in the properties of individual cells and nuclei of organisms may be referred to one of three determining conditions : (i) differences of genotype ; (ii) differences in relation to development or life-history (*i.e.*, in the differentiation in space or time) ; (iii) differences in environment. A fourth condition will later be seen to be important in the special circumstances of germ-cell formation in hybrids—the occurrence of differences between corresponding chromosomes. These conditions must constantly be borne in mind in attempting to analyse the behaviour of chromosomes.

When therefore a particular character in an organism is said to be *due* to heredity or *due* to the environment, or a particular problem is said to be "genetical" or "physiological," the statement is merely relative and depends on convenience of comparison with some ideal or "normal" heredity or environment. This implication is often forgotten because the "normal" condition seems so obvious. Yet it is not at all obvious in cases where a condition of revealing the character is, as is often the case in considering chromosome behaviour, differentiation within the organism. An abnormal property of part of the cells in one organism may be said to be determined by an environmental difference between these cells and the rest of the organism; it may also with equal correctness be said to be determined by a genetic difference between this organism and other organisms. For example, the formation of testes and ovaries by different cells of the same hermaphrodite is primarily a genetic property, just as is the formation of testes and ovaries in different males and females of a species, but while the first is immediately determined by a developmental difference (differentiation) the second is immediately determined by a genetic difference.

Take another instance of great importance in cytology where, after a number of mitotic divisions, a diploid nucleus suddenly divides by meiosis. The difference in behaviour of the nucleus at different times shows it to be subject to differentiation, as are the larger structures. It is also subject to genetic control, as shown by comparison with other organisms having no meiosis. Where, on the other hand, meiosis occurs immediately after fertilisation, it is equally possible to regard it as determined directly by the diploid condition and not by genetically controlled differentiation if it is assumed that all the following mitoses would equally take the form of meiosis in a diploid nucleus (*cf.* Ch. XVI).

Now, our task is to find the materials whose properties answer to the abstract description of the genotype. They must be embodied in "permanent" structures; that is to say, the structures themselves must be stable, and they must be capable of reproducing themselves identically.

These permanent structures are found in the nucleus at the resting stage and in the chromosomes during mitosis. The nucleus and its chromosomes alone amongst visible structures are handed down from cell to cell and from generation to generation in all organisms. In describing them it will be necessary to show their bearing on the genotype and *vice versâ*. For this purpose a point of view is necessary rather different from the usual one, for while the chromosomes contain the " something " which we identify with the genotype they themselves cannot be directly identified with it. Their form and behaviour have special properties of continuity and autonomy, but, as we have already seen in regard to meiosis, they are nevertheless controlled within certain limits by this "something." This also will have to be constantly borne in mind.

(ii) **Conditions of Sexual Differentiation.** Sexual differentiation consists in the production of two different kinds of cells by the species, and this, as already shown, can be attributed to differences in one of three conditions : environment, position in development, genotype. A few examples will provide an illustration of the characteristic way in which these three factors operate.

(*a*) *Environment.* When a fertilised egg of *Bonellia viridis* (Echiuroidea) falls free it develops into a female ; when it falls on the proboscis of a female it develops into a male which is parasitic on the female (Baltzer). Differences of genetic constitution and of position in development therefore have no influence on the kind of gametes produced by the organism. The external environment alone is decisive.

(*b*) *Development.* (*a*) Differentiation in space : in hermaphrodite plants and animals the kind of gamete to be produced by a given mother-cell is determined by its position in the body. In *Actinophrys sol* (Belar, 1926 *b*) the two products of one cell-division remain attached and undergo meiosis side by side, each expelling two " polar bodies." They then fuse, the one which completes its reduction first, taking the initiative. This is the minimum of differentiation and is probably conditioned by difference of position as in a multicellular hermaphrodite. (*b*) Differentiation in time : In some plants or animals (*e.g.*, protandrous Mollusca, *Rana esculenta* and *Cannabis sativa*) the kind of gamete is determined by the period of its development, and an individual, which at one time produces exclusively male gametes, later produces exclusively female.

(*c*) *Genotype.* In *Sphærocarpus Donnellii* (Allen, 1917 ; Lorbeer, 1927) the diploid sporophyte produces two kinds of haploid spores. One develops into prothallia with only female gametes, the other into prothallia with only male gametes independently of any variation in environmental or developmental conditions.

Probably in the sporozoan *Aggregata eberthi* (Dobell, 1925 ; Belar, 1926 *b*) differentiation is of this type. The diploid must be supposed to contain the two dissimilar genotypes, *i.e.*, to be hybrid, and these must separate at meiosis to give the genetically dissimilar haploid cells (*v.* Regeneration). Needless to say, the differentiation only expresses itself in *Sphærocarpus* and *Aggregata* when the germ-cells are about to be produced. The fact that the earlier stages in *Aggregata* are indistinguishable does not show them to be genetically identical as Dobell has supposed (*cf.* Ch. IX).

This classification is sufficient for a large number of cases, but for others a further analysis is convenient. Thus in the Metazoa, not the haploid but the diploid is genetically differentiated in regard to the sex of the gamete produced. And since the two sexes are equally produced by the fusion of the opposite kinds of gametes one of these must be composed genetically of two types. The kind of gamete formed is not therefore determined by its own genetic constitution, but by that of the diploid parent which bears it. The same principle applies to the flowering plants where the properties of the whole haploid generation are similarly determined by the constitution of the parent on which it is, in effect, parasitic. Thus the immediate condition of this differentiation is an environmental difference, but a prior condition is a genetic difference.

The special conditions of haplo-diploid sex differentiation will be considered later.

Since sexual differentiation necessarily restricts the possibility of fusion to gametes of opposite character and therefore often of different origin, other types of differentiation having a *restrictive* effect on fusion are often included with it. Thus in certain Protista, Fungi, and Algæ, fusion is restricted to cells having a different genetic constitution. This is described as " heterothallism " in the

Phycomycetes and Basidiomycetes, and " relative sexuality " in the alga *Ectocarpus* (*cf.* Hartmann, 1929). Such behaviour is analogous in cause and effect with self-sterility in the flowering plants ; all these kinds of " *incompatibility* " demand fusion of gametes that are *genetically* different. The genetical types of gametes are usually of several different kinds, and the system is not alternative. Sexual differentiation, on the other hand, is strictly alternative, and its essential property is the provision of gametes so differentiated as to secure the readiest fusion and most successful development of the product. *Sexual differentiation* demands the fusion of gametes that are *morphologically* different.

Incompatibility and sexual differentiation are therefore distinct in their genetical basis and in their physiological expression. When sexual differentiation comes secondarily to be determined by genetic differentiation, the two agree in securing, wholly or partly, the fusion of genetically distinct gametes, *i.e.*, hybridisation, in a broad sense. The importance of distinguishing them, however, remains, for incompatibility may be superimposed on sexual differentiation of gametes in hermaphrodites and serve the end of encouraging hybridisation where genetic determination of sex has failed to do so.

CHAPTER II

MITOSIS. THE CONSTANCY OF THE CHROMOSOMES

The Resting Nucleus—The Behaviour of the Chromosomes—Abnormal Forms of Mitosis—The Structure of the Chromosomes—Constrictions—Spiral Structure—Permanence and Division of the Chromosomes.

1. THE RESTING NUCLEUS

THE nucleus is a body denser than the surrounding cytoplasm, for in centrifuged cells it passes to the outside. It is also more viscous, and dehydration shrinks it less than the cytoplasm. It is usually globular, except in certain specialised tissues or when it degenerates. It is a smooth-surfaced body with a sharp boundary. Whether this is due to a membrane temporarily enclosing it and distinct from the materials on both sides of it cannot be determined by direct observation, and bio-chemical inference leaves the question unsettled. Micro-dissection experiments, however, suggest that such a membrane does exist.

The living nucleus is often optically homogeneous, but, as will be seen, this does not necessarily imply any physico-chemical homogeneity.

The size of the nucleus is subject to great variation, not only as between different organisms, but also within the same organism. In bulk it may best be compared with the chromosomes into which it resolves itself at mitosis, for these are of constant size. The micronucleus of the infusorian is little if at all bigger than the mitotic chromosomes. The nucleus in the male gametes and in some body cells may be only five or ten times their bulk. But in the egg cells of some of the higher animals and in the vegetative nuclei of pollen grains, for example, the nucleus may be 10^4 or 10^5 the size of the chromosomes (*e.g.*, *Malva*, Nemec, 1910, Tischler, 1923).

Special genetic conditions may affect the relation of the bulk of the chromosomes to that of the nucleus, for in the male bee with half the number of chromosomes of the female the nuclei are of similar size in corresponding cells (Nachtsheim, 1913, *cf.* Schrader and Hughes-Schrader, 1931 ; Torvik, 1931 ; *v.* Ch. VII).

This variation in size bears some relation to the variation in size of the cell in the same organism (the Kern-plasma ratio). When different organisms are considered the volume relationship is apparently subject to genetic control (*e.g.*, *Tradescantia*, Ch. III, Fig. 9). Under the same genetic conditions doubling of the size of the nucleus (by doubling the number of its constituent chromosomes) leaves the volume relationship unchanged in most cases, and, where this is not so, the difference may be described as due to a lack of complete elasticity in the organism in regard to cell-size variation (Ch. VIII).

In almost all resting nuclei are embedded one or more amorphous, spherical or occasionally rod-shaped bodies of higher density and refractiveness than the surrounding ground substance (Fig. 2). These are called nucleoli. They occupy in all not more than one-twentieth to one-fiftieth of the total volume of the nucleus and characteristically lie away from the surface. As a rule they break up and gradually disappear as the nucleus begins to divide, *i.e.*, at prophase, and are reconstituted at the beginning of the next resting stage. They are therefore supposed to have no genetic significance.

It is probable that as a rule the nucleoli remain constant in number until the end of the resting stage. De Mol (1928) found that, in the root-tip nuclei of hyacinths with 16, 24 and 30 chromosomes (where the nuclei were proportionate in size to the number of chromosomes) the maximum number of nucleoli was almost invariably 2, 3 and 4 respectively. When the nucleus grows, the nucleoli increase in bulk more or less in proportion.

Owing to its greater density the nucleolus may be expelled from the nucleus by centrifuging (Andrews, 1915 ; Nemec, 1929 *a*). It may then persist in the cytoplasm as long as twenty-seven days, and only gradually disappear.

It has been supposed, on a domestic analogy, that the nucleoli serve as a store of material used by the chromosomes as they go into division. This hypothesis is thought to be supported by the observation that the ends of the chromosomes stick to the nucleoli at prophase (Navashin, 1925; Sorokin, 1929), or by the observation of a continuity in staining reaction between chromosomes and nucleoli (Zirkle, 1928, 1931). But it is to be expected that with the least collapse of the ground substance in fixation the more viscous bodies (nucleoli and chromosomes) will be brought into contact; and an identity of fixing and staining reactions at different stages of mitosis is not a proof of chemical or structural identity. *A fortiori*, one is not to be misled by "the appearance of nucleolar material flowing into the spireme" (Zirkle, 1928; *cf.* Martens 1928).

We must admit that at present no plausible function has been found for the nucleoli, and we may for most purposes consider them merely as fragments of cytoplasm having no function, included in the nucleus by chance between the chromosomes as they pass into the resting stage, and altered—especially dehydrated—owing to their special surroundings. This view seems to be supported by the observation that the nuclei lacking nucleoli are the smallest, the micronuclei of infusorians (Belar, 1926 *b*). In larger nuclei it might be thought that the nucleoli would serve to increase the ratio of surface to effective volume, but in this regard their bulk is as a rule negligible.

In the Protista, nucleoli vary greatly in form, position and behaviour (*cf.* Belar, 1926 *b*). In some species, nucleoli may lie on the periphery of the nucleus (*e.g.*, *Amœba terricola*). In other species they are numerous and rod-shaped, resembling chromosomes (*e.g.*, *Euglypha*). In others again an internal structure can be distinguished (*e.g.*, *Chilodon*).

The nucleoli are occasionally found to persist to metaphase of mitosis. Sometimes this is clearly abnormal, as in the gametophyte (pollen grain) of hybrid plants (D., 1929 *c*, in *Tradescantia* spp.). Sometimes it is characteristic of a species, especially in the lower organisms, and the nucleoli may be extruded into the cytoplasm and lost, or even divide and pass into the daughter nuclei (Belar 1926 *b*, *Chlamydophrys Schaudinni*). In the higher plants, *e.g.*, in *Zea Mays*, these bodies degenerate on reaching the poles and do not enter the new nuclei (Yamaha and Sinoto, 1926; Zirkle, 1928, 1931). Such bodies in *Amœba verrucosa* have been called "chromatin nucleoli," but we need not ascribe any special virtue to this persistence; conditions external to the nucleus such as might determine a rapidity of prophase changes or a greater viscosity of the nucleus, as Belar suggests, may be held responsible.

A special abnormality is found in the coleopteran *Dytiscus* (Giardina, 1901; *cf.* Boveri, 1904; Günthert, 1910). Here material is expelled from an oögonial nucleus four divisions before meiosis. This material is transmitted with one of the daughter nuclei at each division, until the last when the nucleus with nucleolar material serves as the oöcyte while the other fifteen have a merely nutritive function. This process has been described as a "chromatin-diminution" (*q.v.*), but the substance expelled cannot be regarded as an essential part of the hereditary material, and it is more likely to be of nucleolar origin.

2. THE BEHAVIOUR OF THE CHROMOSOMES

(i) **Introduction.** Nuclei divide by the characteristic process of mitosis. Recent work, particularly on the Protista, has shown that certain features, precisely those of genetic significance, are universal. Mitosis can accordingly be defined by its essential properties as: *the separation of the identical halves of the longitudinally split chromosomes constituting a nucleus into two identical groups which constitute two daughter nuclei.* Consequently it may also be said that mitosis is the process by which a nucleus gives rise to two daughter nuclei each morphologically equivalent to one another.

The longitudinal splitting of the chromosomes was first observed by Flemming in 1880. Its physiological meaning was pointed out by Roux in 1883: if equivalent nuclei can only be produced by such longitudinal splitting then the chromosomes must be longitudinally differentiated in their physiological properties. Experiment has now shown this conclusion to be valid (*v.* Ch. IX).

There are two kinds of nuclear division: simple mitosis and double mitosis associated with the reduction in the number of the chromosomes; this is merely an abnormality of the simple mitosis, but it is convenient on account of its special character to refer to it as *meiosis* in contradistinction to mitosis, the normal type which we are now going to consider.

(ii) **Prophase.** The prophase of a mitotic division is first indicated by the appearance of coiled, contorted threads which as a rule, but not always, fill up the whole body of the nucleus. These structures can be observed in living cells as well as after fixation and staining (Plate VIII, *cf.* Lucas and Stark, 1931) although in living material the nucleus first appears granular. The granulation is reasonably supposed to represent an optical section through the coiled threads which are later clearly distinguishable (Belar, 1929 *b*).

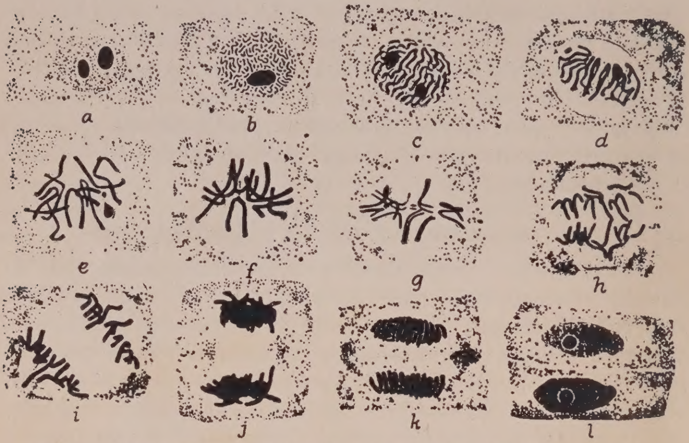


FIG. 2.—Side views of mitosis in root-tip cells of *Allium cepa*. *a* Resting nucleus, two nucleoli. *b* Beginning of prophase. *c* Later prophase, chromosomes clearly double. *d* Chromosomes beginning to lie nearer the equator. *e* Early metaphase, nucleolus disappearing. *f, g* Metaphase. Chromosomes all lying with their spindle attachments in the equator. *h, i* Anaphase. *j, k, l* Telophase. The complete set of chromosomes is not shown in all cells ; the sections are cut at 6 μ (From Belar, 1926.)

In the most favourable material it is possible to see at the earliest stage that the threads are double, and it is probable therefore that this is their universal characteristic throughout prophase (Ch. XI). The double threads can be traced in their development until metaphase, when they are recognised as chromosomes. The two single threads of which they are composed may be described as chromatids. This term was originally used by McClung to describe the single threads at meiosis, but since the single threads (being half-chromosomes) correspond in every way at the stages when they occur in the two types of nuclear division there can be no objection to calling a half-chromosome a chromatid both at meiosis and at mitosis.

Following their appearance the chromosomes contract lengthwise, and to a slight extent in gross bulk. They are evidently more viscous owing to loss of water, and they appear to suffer less from the action of fixatives. During the resting stage the nucleus has probably been uniformly filled with the material of the chromosomes. Loss of fluid by the chromosomes therefore merely means that the nucleus becomes differentiated into chromosomes and "nuclear sap."

It was formerly held that at this stage the chromosomes were united end to end to form one "continuous spireme." It has now been shown in all clear cases (and especially at meiosis, on which great attention has been concentrated) that this is not so (*cf.* Fig. 20). As mentioned above, the free ends of the chromosomes must be particularly liable to collapse in fixation. Observations of discontinuity are therefore necessarily more significant than observations of continuity, which are characteristic of defective treatment (*v.* Appendix I). The assumption of a continuous spireme is therefore unjustifiable on cytological grounds. On genetical grounds it is equally unjustifiable, for the constant production of a single continuous ring requires the secondary assumption of a temporary *specific* attraction between dissimilar pairs of ends of chromosomes. This assumption is contrary to the principles of chromosome mechanics (*v.* Ch. XIII) and breaks down when applied to hybrids and polyploids and cases of interlocking at meiosis (*q.v.*). A genuine continuous spireme probably occurs under special conditions in the coccid *Icerya purchasi* (Hughes-Schrader, 1927).

The chromosomes now have a non-uniform granular structure. This is most clearly observed at meiosis (*cf.* Wenrich, 1916; Gelei 1921; and *v.* Ch. IV). Each thread then consists of a series of particles of different sizes called chromomeres, connected by a less deeply staining thread. The linear arrangement of the chromomeres in different nuclei is constant. It seems unlikely that these delicate structures are uninjured by fixation ; no doubt their discontinuity is exaggerated. But their constancy shows them to be significant, as well as characteristic, artefacts (*v.* Appendix I). It is therefore difficult to regard them, as Kaufmann has suggested (1931), merely as twists in the chromatid. They demonstrate morphologically the linear differentiation of the chromosome. And it is important to notice that the two chromatids correspond exactly. Since, as we shall see, they must be supposed to arise from the longitudinal division of one, that division has been, so far as cytological evidence can show, into two identical halves. This identity is preserved from the time the doubleness is first seen at prophase throughout all stages of mitosis and all succeeding divisions of the chromatids at succeeding mitoses.

Further linear contraction of the chromosomes is accompanied by an increase in their thickness. There is no direct evidence as to what change takes place in the internal arrangement of the chromosomes, but indirect evidence suggests that it is due to the gradual assumption of a spiral form by the chromatid (*v. infra*). The increase in thickness obliterates the distinction between chromomeres and the chromatids gradually assume a rounded outline and eventually a highly uniform cylindrical structure, apart from constrictions, which will be considered later.

In most organisms contraction of the chromosomes reaches its maximum at the last stages of prophase. They are now probably one-tenth or one-twentieth of the length they were at the earliest stage of prophase. The two chromatids of each chromosome lie parallel and in close proximity to one another.

(iii) **Metaphase : the Spindle.** Outside the nucleus, in most animals and in many of the lower plants, but not in the higher plants, lies a body which is actively concerned in the division of the nucleus. This is the centrosome. It consists in the resting stage of a small double granule which is usually capable of differential staining and has divided during the previous nuclear division. There has often been difficulty in following its history, but it would appear from Boveri's studies that it is transmitted solely by the sperm of which it constitutes the " middle-piece," the centrosome of the egg-cell degenerating in sexual reproduction. Where the egg develops without fertilisation its own centrosome continues to function, unless the sperm enters the egg (*e.g.*, in *Rhabditis*, Belar, 1924).

When a centrosome is present it develops radial striations, " the centrosphere," in the cytoplasm around it, during prophase. Its two halves pass to opposite sides of the nucleus, and it is between them that there arises a spindle-shaped portion of the cytoplasm more " viscous," or at least containing less water, than the rest, usually enveloping the nucleus and eventually taking its place in the cell.

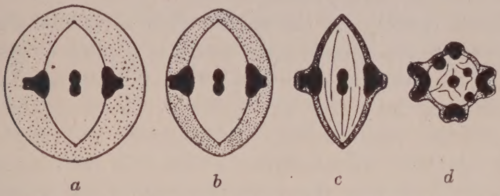


FIG. 3.—Diagram to show the effect of dehydration on the different cell constituents at metaphase of mitosis or meiosis. Chromosomes black, cytoplasm stippled, spindle clear. *a* In isotomic solution. *b*, *c*, *d* In hypertonic solution, successive stages of dehydration. *a–c* axial section ; *d* equatorial section. (From Belar, 1927.)

When no centrosomes are present the spindle may arise in the same way as it would if they were present, *i.e.*, between two points on opposite sides of the nucleus. Alternatively it may arise between several " poles " which by fusion are later reduced to the normal two. When two sperms fuse with one egg, three or four centrosomes are present, which give rise to a multipolar spindle and irregularity in the distribution of the chromosomes (*v.* Ch. IX). In the protozoan *Acanthocystis* (*cf.* Belar, 1926 *b*) centrosomes are present having the static functions and appearance of other centrosomes, but apparently no necessary connection with spindle formation.

The " viscosity " or rigidity of the spindle may be inferred in three ways (Belar, 1929, *a* and *b*). When the cytoplasm is shrunk by dehydration of living cells in a hypertonic solution, as in the course of fixation or in special experiments, the spindle shrinks less than the rest. When living cells are smeared on a slide in a single layer, as is readily done when the cells are large, they lie with spindles flat; since the cells are globular the spindles must have opposed special resistance to pressure. Finally the spindle is seen to be more refractive to light than the rest of the cytoplasm.

The same tests show the relative rigidity of different cell organs. The nuclear ground substance at late prophase is less rigid than the spindle; the chromosomes at late prophase and metaphase are more rigid. The detailed consideration of these properties does not concern us here (*cf.* Gray, 1931).

The special rigidity of the spindle is of a peculiar kind. The shrinkage when the spindle loses water is greater crosswise than axially. It may thus be caused to split axially either in numerous small fissures or in a few broad clefts. These, especially when stained, give the spindle a striated appearance, and they have been described as the "spindle-fibres." What is their significance? Clearly they show that the water content of the spindle is not evenly distributed but must be concentrated in axial channels between the more rigid portions of the spindle. This is shown equally by the special axial expansion of the spindle at a later stage. There are therefore in the spindle axial structures of high rigidity which may be described as fibres, although the "fibres" that are seen are merely the channels between them. Their structure is not inherent in their materials like that of the fibres of connective tissue; it must be determined by special conditions external to them, as is the structure of fibrillæ or cilia in the Protozoa or the arrangement of iron filings in a magnetic field. This has been shown most clearly by Chambers; a needle passed through the spindle at metaphase does not disturb the chromosomes to which *connective* fibres might be supposed to be attached. The spindle as a whole in fact owes nothing to the materials from which it is derived—these seem to be indifferently cytoplasm or nuclear substance. It owes everything to the temporary external conditions of mitosis.

During the prophase the chromosomes have been disposed evenly throughout the nucleus. As the spindle envelops the nucleus and its boundaries disappear the chromosomes come to lie midway between the two poles of the spindle in a flat "plate" on which they distribute themselves evenly. Comparison of different organisms shows that this distribution depends on one point in each chromosome lying on the equator of the spindle. This point of "attachment" to the spindle may be terminal or intercalary. The parts of the chromosomes near the point of attachment are spoken of as "proximal," those further away as "distal." Where the chromosomes are short they may lie entirely in this plane as though in a flat plate. Where they are long, relative to the size of the spindle, the limbs of the chromosomes remote from the attachment lie at random—equatorially or axially. But owing to the spindle space being limited, the limbs of long chromosomes on the edge of the spindle lie in the outer cytoplasm, and the bends at their spindle attachments therefore point inwards. In cells of exceptional shape such as pollen tubes the chromosomes may be disposed less regularly in a way that scarcely suggests the characteristic plate. In many animals, all or most of the points of attachment lie on the periphery of the spindle; the distal parts of the chromosomes then lie wholly outside the spindle, and in living cells (*cf.* Belar, 1929, *a* and *b*) can be seen to float in the streaming cytoplasm. In this way the chromosomes may fill up the greater part of the cell space.

Until metaphase, the chromatids are held together less closely elsewhere than at the spindle attachment. The momentary condition of "full" metaphase is reached when the limbs of the chromosomes have come together as closely throughout their length as they were earlier at the point of attachment. It is commonly imagined that the stage with the distal parts of the chromosome separate follows this stage with the closest association, and is actually the first stage in the separation of the chromatids. This is not so. Separation always begins at the point of attachment, at a time when the distal ends are more closely united than earlier, and a wide separation of the distal ends shows an *early* metaphase stage, not a late one (*cf.* Fig. 16).

(iv) **Anaphase.** The chromatids move apart (or are pulled apart) towards opposite poles as though attached to these poles at the spindle attachment (*v.* Belar, 1929 *b*, and Fig. 16B). The chromatids remain in close contact at their ends until the anaphase separation finally draws them apart. It is common to refer to the separation of the chromatids as the " division " of the chromosome, but, as we have already seen, the division has taken place much earlier, and, throughout the prophase, chromatids have been merely held together either by a common pellicle surrounding them or, more probably, by a specific attraction existing between them. At anaphase therefore it is an attraction which has to be overcome rather than an intricate connection which has to be severed. (The relations of the chromatids at meiosis cannot be understood unless this principle is grasped.)

When the separation is complete the corresponding groups of chromatids, now called " daughter chromosomes," pass towards opposite poles. This movement has been analysed by Belar with remarkable success, working with living cells (1927, 1929, *a* and *b*). In the first part of the movement the spindle undergoes no important change in shape or character, and it appears that the movement is independent of external variations that can be brought to bear on it experimentally. To this extent it may be said to be " autonomous." At late anaphase the situation is entirely different. There is little evidence that the chromosomes move any further through the spindle, but the spindle itself changes shape. The middle part, between the separated bodies of chromosomes, expands lengthwise and contracts correspondingly crosswise so that the chromosomes are pushed apart and the anaphase movement completed. Belar maintains that this is an inherent and " active " property of the spindle itself, more especially because with dehydration in hypertonic solutions the stretching of the spindle is exaggerated. Probably it is a property correlated with the special distribution of its water content. Where, in meiosis in *Stenobothrus*, one pair of chromosomes in separating offer, on account of their greater length, more resistance to separation than the rest, the whole spindle is tilted evenly. This argues not merely pressure from the middle part of the spindle but an independent coherence of the middle part and of the polar parts. Where the chromosomes are very long, as in mitosis in *Tradescantia* and *Aggregata*, the separation of the two bodies of chromosomes is assisted by a further linear contraction of the chromosomes at late anaphase.

PLATE I

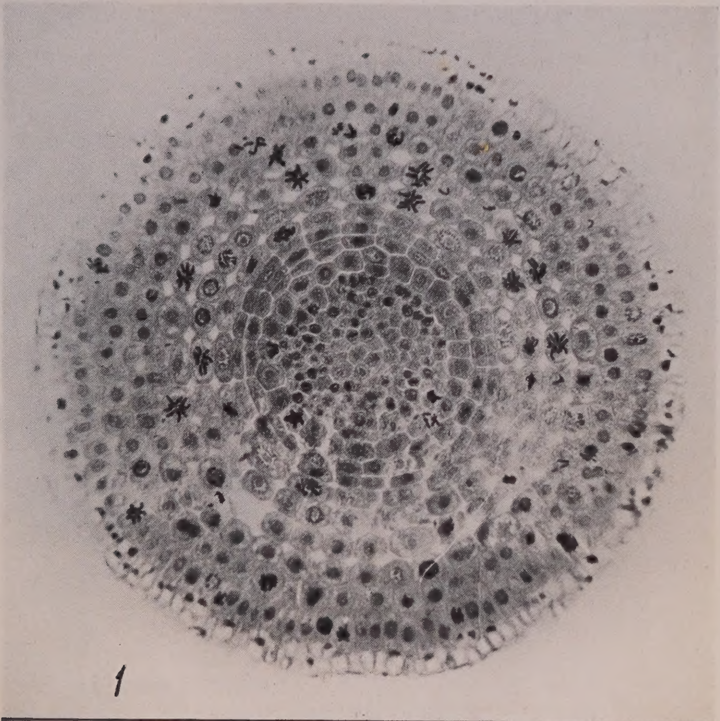
MICROPHOTOGRAPHS REPRODUCED BY KIND PERMISSION OF DR. M. S. NAVASHIN

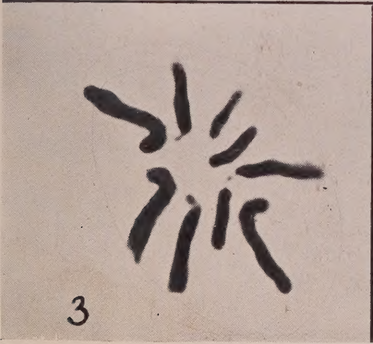
FIG. 1.—Section of root-tip of *Crepis dioscoridis*, $2n = 8$. Notice the four chromosome types in all metaphases, and also various stages of prophase and telophase of mitosis. × 250.

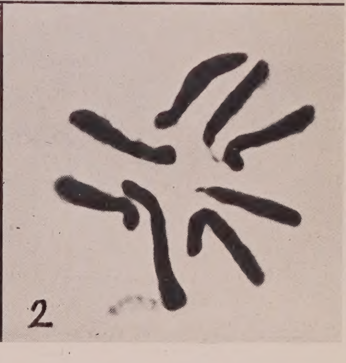
FIG. 2.—Outer metaphase plate at 1 o'clock in Fig. 1. × 2300. The chromosome lying right and left at 6 o'clock in the plate is from another cell and is out of focus in this photograph.

FIG. 3.—Metaphase of mitosis in root-tip of triploid *Crepis capillaris* ($2n = 3x = 9$). Of the three D chromosomes one has a large trabant and two a small one. × 3000 (*v.* Text).

PLATE I


1


3


2

[*To face p.* 26.

Aberrant numbers of chromosomes found at mitosis show that occasionally both halves of one chromosome by accident pass to the same pole, giving daughter groups, one with one too many, one with one too few, chromosomes (*cf.* Mohr, 1931). It probably also happens (especially in callus formation in plants, and in abnormal tissues in animals where division is very rapid) that the two groups fail to separate, and a single daughter nucleus is reconstituted with the double number of chromosomes. Neither of these processes has been observed in its entirety, but conditions that would result from them have been found and are important in connection with the origin of polyploidy and polysomy (*q.v.*).

(v) **Telophase.** When the chromosomes reach the pole they contract longitudinally and form a compact mass which passes through stages more or less comparable with the reverse processes of prophase. These appear to consist essentially in the imbibition of water. In some organisms the chromosomes form separate vesicles at first (Belar, 1928 *b*, Fig. 42), and where the resting stage is short these may persist, separately identifiable, to the next division (*v. infra*).

(vi) **Duration of Mitosis.** The duration of successive stages of mitosis has been recorded from observations of living cells by Belar (1926 *b*, 1929 *b*, *Tradescantia*) and others. The following observations indicate the range of variation found, but do not include either the quickest or the slowest examples. The third case is an observation of meiosis, which will be specially considered later.

TABLE 2

The Time Taken by Division

	Prophase.	Beginning of Metaphase.	Metaphase.	Anaphase.	Beginning of Telophase.	Telophase.	Total.
Protozoan (mitosis) :							
Rhogostoma schüssleri . .	6′	2′	2′	·5′	2′	20′	32·5′
Euglypha sp.	40′	7′	18′	6′	8′	100′	179′
Plant (mitosis) :							
Tradescantia virginiana . .	181′	10′	4′	15′	130′		340′
Animal (meiosis, first division) :							
Stenobothrus lineatus . .	—	—	6′	42′	39′	60′	—

3. ABNORMAL FORMS OF MITOSIS

Deviations from the described type of mitotic division are found in the higher plants and animals, but they are nowhere such as to render the process unrecognisable. In the lower organisms marked deviations from the described type occur. Many of these are described by Belar in a comprehensive survey of mitosis in the Protista (1926 *b*).

In many Fungi and Protista, an intranuclear spindle is found. In this type the centrosome, which is characterised by the presence of permanent granules colourable with nuclear stains, may lie outside the nucleus, as in some *Amœbæ*, or inside it, as in the protozoan *Euglypha ;* in the Fungi and many Protozoa the centrosome normally appears only at division.

Another type of abnormality is the extreme reduction in the size of the spindle relative to the nucleus. In this type, if the spindle is still distinguishable, it lies to one side of the dividing nucleus, as in *Aggregata eberthi* (Fig. 6). This organism demonstrates two other peculiarities of mitosis. It undergoes a process of " multiple nuclear division " during spore and germ-cell formation. In other organisms the relationship of this process to true mitosis is still obscure. Here the chromosomes do not show the high degree of contraction characteristic of metaphase. They retain the length and appearance normally seen at early prophase, contracting further at anaphase. Divisions follow one another rapidly, however, and this further contraction is not always completed, so that the ends of two chromosomes which are longer than the rest do not separate. In this way daughter nuclei are constituted which run into one another and suggest the appearance of simple fission of a nucleus—what has always been called " amitosis." None the less the actual longitudinal splitting of the chromosomes can be seen with the utmost clearness, and in later divisions this separation is completed (*v. infra,* Fig. 6).

These examples merely indicate the wide range of structure and mechanism and the deceptive appearance that is found at mitosis in the Protista. They account for the difficulty in interpreting mitosis in these organisms and for its earlier description as " amitosis," that is, a type of division in which the chromatids of each chromosome were not separated to opposite daughter-nuclei. Extreme examples of this difficulty are seen in *Vahlkampfia* (*cf.* Belar, 1928 *b*) and in *Amœba* (Belar, 1926 *b*).

Improvement in technique in the Protista and elsewhere now makes it possible to show that all nuclear division is normally mitotic and that the apparent contradiction of genetic principles in the occurrence of amitosis need no longer be taken seriously. Amitosis, the division of a nucleus without the separation of chromatids, is only found in short-lived tissues, such as the endosperm of seed-plants and the deciduous embryonic membranes of animals, when it is frequently unaccompanied by cell-division. It does not therefore give rise to independent and equivalent daughter-nuclei.

There is one apparent exception, the division of the macronucleus in the Infusoria. Here many forms of division are found which can scarcely be reconciled with the principles of mitosis (*e.g.*, *Spirostomum*, *cf.* Belar, 1926 *b*), and others which appear as very degenerate mitoses (*e.g.*, *Spirochona*). But the macronucleus of the infusorian is in a sense analogous with the body-cell nucleus in a multicellular organism, and as in *Ascaris* it need not carry the whole of the hereditary material, resulting from accurate mitotic division. It is off the germ-track and cannot give rise to a micronucleus, which alone is capable of reproduction by conjugation. Its life is of restricted duration, for at intervals in the absence of sexual reproduction, when it always degenerates, it disappears and is replaced by a new macronucleus derived directly from its sister micronucleus by division and the growth of one of the products (Woodruff and Erdmann, 1914, on *Paramœcium*). Belar (1926 *b*) is inclined to believe that reported cases of a micronucleus arising from a macronucleus are due to the smaller nucleus being temporarily included in the larger and overlooked at division. Races genuinely devoid of a micronucleus are apparently incapable of undergoing sexual reproduction (Woodruff and Spencer, 1922).

When the macronucleus suffers an unequal division as in amitosis, we may therefore suppose that it suffers an irreversible change, as does the nucleus of *Ascaris* undergoing chromosome diminution (*q.v.*). And such a change cannot be undergone by a nucleus retaining the full genetic potentialities of the species (*cf.* Ch. IX).

Summing up, recent work leaves no doubt that: whenever a nucleus divides to produce two daughter-nuclei physiologically or morphologically equivalent to it, it does so by mitosis. Further, the effective test of a nucleus is not so much in its chemical or physical properties, but in its behaviour: *a nucleus is a cell-body which arises or reproduces by mitosis.*

4. THE STRUCTURE OF CHROMOSOMES

(i) At Prophase: Spiral Structure. At metaphase all chromosomes consist of two cylindrical rods, the chromatids, which are normally of even diameter. This diameter is a racial characteristic constant for all the chromosomes of a complement except such as may be less in bulk than a sphere of the specific diameter (*v.* Fig. 4).

Variation in the apparent diameter of the chromosome is due to, first, the pairs of chromatids being seen sometimes endways-on, *i.e.*, in the same line of vision, as is always the case at the attachment in

TABLE 3

Estimated Total Lengths of Chromosomes in Complement (in Microns)

	Stages of First Division of Meiosis.					Mitotic Metaphase*
	Leptotene	Pachytene	Diplotene	Diakinesis	Metaphase	
Lilium species . . . *n* = *12*, Belling, 1928, *c*†	—	1,469	257	152	152	—
Aloë purpurascens . . *n* = *7*.	—	545	—	55	—	—
Bellevalia romana . . *n* = *4*. Dark, unpublished (*v.* Fig. 20)	—	386	—	—	41	63
Dendrocœlum lacteum . *n* = *7*. Gelei, 1921.	421	—	—	—	—	86

* This length is halved to correspond with the haploid complement measured at meiosis.

† Belling states (1931 *a*) that leptotene threads in *Lilium* are six and a half times as long as at metaphase. This seems to disagree with the results recorded here.

polar views, and sometimes sideways-on, when the chromosome will be just twice as broad ; and, secondly, the occurrence of constrictions (*v. infra*).

Now each of the cylindrical rods is the product of a linear contraction of the threads observed in early prophase. The extent of this contraction can be approximately estimated from measurements. The rather fragmentary estimates given are largely derived from observations of successive stages at meiosis, where the contraction at metaphase is greater than at mitosis (*cf. Bellevalia*), but they indicate the extent of the changes undergone during the prophases of both types of division (Table 3).

The degree of contraction at metaphase is, however, subject to genetical control, as will be seen later (*v.* Ch. III), and may therefore vary considerably in any group. It is probable also that the degree of contraction already reached at pachytene varies in different organisms.

In this process of contraction we may probably distinguish three kinds of change in succession. First, there is the change which renders the chromosomes visible at the end of the resting stage. This may be regarded as a dehydration of previously more dispersed chromatin material, associated (according to Sakamura, 1927) with an increase in hydrogen-ion concentration in the nuclear sap.

Secondly, there is a linear contraction of the thread such as might be regarded merely as due to the successive chromomeres coming to lie closer together. But since the separation into chromomeres is probably to some extent an artefact (although characteristic and significant) such a simple contraction need not necessarily be distinguished from the third change. This evidently consists in a spatial rearrangement of the thread. The rearrangement might be supposed *a priori* to be orderly or haphazard. Since each chromatid is uniformly cylindrical at metaphase, there seems no arrangement that can be assumed but an orderly one, and none of this kind but a spiral. Such an arrangement was first observed by Baranetsky in 1880, and his observations have since been generally confirmed whenever any definite structure has been observed in the chromosomes of plants or animals. But these observations depend on a special technique of treatment, and are therefore necessarily confined as yet to a few organisms, mostly organisms with large chromosomes, as follows (*inter alia*).

Table 4

Observations of Spiral Structure

(*a*) Prophase of mitosis.	Kuwada (1921), *Phrynotettix, Vicia.* Newton (1924), *Galtonia.* Kauffmann (1926), *Tradescantia.* de Winiwarter (1931), *Tettigonia* (*cf.* Ch. XIII).
(*b*) Interphase between meiotic divisions.	Newton (1927), *Tulipa.* Taylor (1931), *Gasteria.*
(*c*) Prophase of meiosis (diplotene).	Babcock and J. Clausen (1929), *Crepis.*
(*d*) Metaphase of first meiotic division.	Taylor (1922), *Gasteria.* Sakamura (1927, *a* and *b*), *Tradescantia.* Kuwada and Sakamura (1926), *Tradescantia.* Maeda (1928), *Lathyrus.* Shinke (1930), *Zebrina, Lilium.* Sax (1930), *Secale, Lilium.* Tuan (1931), *Gasteria.* Darlington (Plate II), *Hyacinthus.*
(*e*) Resting stage before meiosis.	Janssens (1924, Fig. 221), *Stenobothrus.*
(*f*) Anaphase of mitosis in root-tip.	Kuwada (1926), *Vicia.* Kuwada and Sugimoto (1926), *Vicia.*
(*g*) Prophase of supernumerary mitosis (pollen grain).	Beadle (1931), *Zea Mays* (*cf.* Ch. XIII)

These observations have been especially facilitated by the smear method of fixing pollen mother-cells, in two ways, either of which gives an artefact (*v.* Appendix I), which is characteristic of the metaphase chromosome, and, since it agrees with anticipation in showing the spiral structure, is probably the basis of a sound interpretation. One method, used by Sakamura (1927 *b*, *v.* Plate II), is to fix the material in boiling water. Another, which gives occasional but not systematic success, is to press the chromosomes in smearing the cells, which are afterwards ordinarily fixed and stained (Plate II). The three conditions under which the spiral structure is best seen are (i) in a static condition at metaphase, with this special treatment ; (ii) at telophase, while recovering from the spiral condition after division ; (iii) at prophase, after a curtailed resting-stage, as in the second meiotic division, in a pre-meiotic division where a sex chromosome does not go into a complete resting stage, or in polymitotic maize; in these circumstances the spiral from the preceding division is seen to persist.

The interpretation of the structure, when exactly stated, has usually been that the chromosome consists of one spiral which may be single, or, according to Sakamura (1927), internally to the spiral, double. This, as Kuwada and Sugimoto have pointed out (1926), is in flagrant contradiction with the general observation that the metaphase chromosome, whether at meiosis or mitosis, consists of two rods, the chromatids, which are distinctly separated at an earlier stage and must be derived from the contraction of two separate threads (*v.* Ch. IV). Examination of the photographs will show the source of this contradiction. What appears to be a single spiral when considered as a perspective view is undoubtedly two separate spirals when considered as an optical section (when both chromatids are lying in the same focus). The perspective interpretation leads to various other contradictions. The chromosome sometimes seems to be of a zigzag structure (Belling, 1926), and when apparently a spiral, the spiral may appear to reverse its coiling (Sax, 1930). This is no doubt due to one of the spirals being taken as the continuation of the other. Each *chromatid* is therefore one spiral, and there is no reason to doubt that this spiral is single and turns in one direction (*v. infra*).

There are other observations of structure at metaphase which can scarcely be taken as characteristic (*cf.* S. Navashin, 1910; Sands, 1923). Especially is this true of chromosomes which have been pressed *after* they have been fixed and have become brittle (Belling, 1926). The discontinuity then observed, although doubtless influenced by any discontinuity in the living chromosome, might equally be expected in homogeneous material.

Evidence of another kind on the structure of the metaphase chromosome is afforded by the observations on normally treated material. First, it is seen that in optical section the chromatids, especially at the ends, are often double at metaphase and anaphase. Secondly, very small trabants (*v.* Fig. 4) are found in *Tradescantia* to be attached not to the middle of the end of the chromosome but to its edge. Both of these observations can be attributed to the structure of the chromatid being cylindrical, and perhaps (after fixation) hollow. But, again, the optical section has often been interpreted as a perspective view, and this has led to the erroneous belief that the daughter chromosome has already divided, for the next division, at anaphase (*cf.* Section (iv)).

(ii) **At Metaphase and Anaphase : Constrictions and Trabants.** In the course of prophase, after the chromomere structure has disappeared, another kind of discontinuity appears in the chromatin thread in many organisms. This is at first an unstained gap in the chromatid ; afterwards it develops into the metaphase "constriction," at which the cylindrical body of each chromatid is drawn together as a sausage is drawn together with string or a blood vessel ligatured. All chromosomes have one such ligature in their structure, unless the constriction is terminal—the "attachment constriction." But there are also found in many chromosomes "secondary" constrictions which have no relationship with any present spindle attachment (*cf.* Plate II and Fig. 4).

The spindle attachment has the following four characteristics distinguishable at metaphase :—

(*a*) It always coincides with a constriction. At such a point the chromosome is more easily bent and stretched. This has been shown by micro-dissection (Chambers and Sands, 1923), and is equally evident from comparative observation of chromosome form in fixed material. The constriction is a point of weakness in the chromosome. Secondary constrictions share this property. The chromosome, therefore, in the absence of secondary constrictions consists of two limbs when the attachment constriction is intercalary, and one when the constriction is terminal.

(*b*) During metaphase the two chromatids lie at this point in the axis of the spindle, although elsewhere lying at random. The chromosome seen in polar view therefore seems narrowest on either side of the attachment constriction.

(*c*) The two chromatids are held together tightly at this point, although elsewhere lying loosely parallel. The ligature may occur at one point, or may be extended so that a definite non-staining gap occurs in the chromosome. This also applies to secondary constrictions.

(*d*) Its position is sometimes marked by a granule which can be

PLATE II

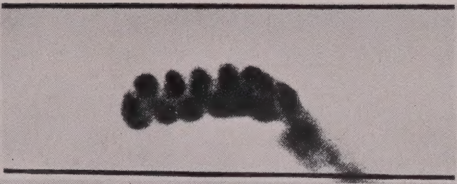
Fig. 1.—Part of a univalent chromosome at first metaphase of meiosis in *Hyacinthus orientalis*, pressed in fixation to show spiral structure of two chromatids side by side. × 5000. (D., unpublished.)

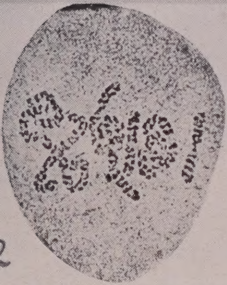
Figs. 2 and 3.—Chromosomes at first metaphase in *Tradescantia virginiana*, fixed in boiling water and unstained, to show spiral structure. (Sakamura, 1927.)

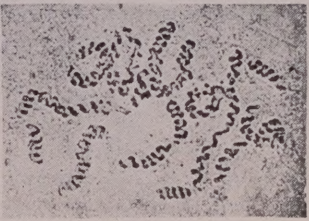
Figs. 4–9.—Mitosis in root-tips.

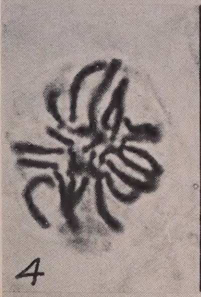
Figs. 4–6. Three clonal forms of *Tulipa Clusiana* ($x = 12$), diploid, tetraploid and pentaploid. Figs. 7 and 8. *Aconitum Napellus carneum*, two photographs of the same metaphase, $2n = 32$. × 1800. Fig. 9. *Digitalis mertonensis*, $2n = 112$. × 2500 (*v.* Chap. VII, from Buxton and D., 1932).

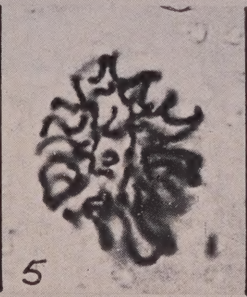
PLATE II

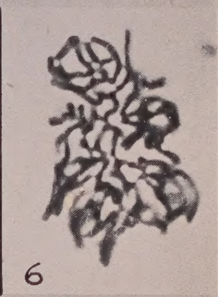

1

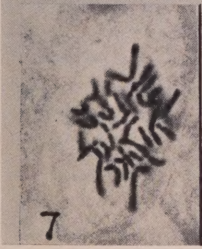

2

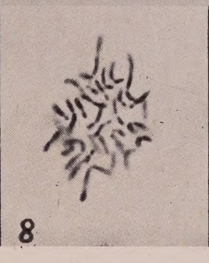

3

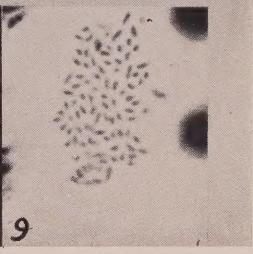

4


5


6


7


8


9

[*To face p.* 34.

more sharply stained than the rest of the chromosome—the polar granule (*cf.* Wenrich, 1917 ; Janssens, 1924 ; Belar, 1928 *b* ; Belling, 1928 ; and Kuwada, 1929).

Constrictions give great diversity to the form of the metaphase chromosomes, and being constant in position and length they also give character to the individual chromosomes. Their study therefore has been of the greatest importance in investigating constancy and variation in mitotic chromosomes within and between species and between parents and their own gametes or gametophytes, particularly in the flowering plants (*e.g.*, in *Crepis*, *Vicia*, *Tradescantia*, *Muscari*, *Tulipa*, *Drosophila*). This advance we owe in the first instance largely to the work of S. G. Navashin and his school, and later to Sakamura (1915 *et sqq.*), Taylor (1922 *et sqq.*), Newton (1924, 1927), M. Navashin (1926, 1927, 1929), Delaunay (1926, 1929), Lewitsky (*loc. cit.*). *Cf.* also Belar (1926), Bridges (1927), Kachidze (1929), Babcock and Hollingshead (1929).

The following are the main conclusions which are applicable to the higher plants in general (*cf.* Delaunay, 1929).

(*a*) Each chromosome has an attachment constriction and perhaps one or more secondary constrictions which are constant in position. While the attachment constriction may have any position, terminal or intercalary, in the chromosome, the secondary constrictions are never terminal.

(*b*) Constrictions vary in the length of the lacuna they create. This length is a characteristic property, although subject to variation as an artefact, and, in part, as a natural condition. We may therefore speak of a " long " constriction and a " short " constriction. The real variation in appearance is general amongst very long constrictions, especially those separating trabants (*v. infra*). Long constrictions may be two or three times as long as the chromatid is broad. At anaphase all constrictions are liable to be emphasised by the tension between the attachment and the parts of the chromosome distal to the constriction. Attachment constrictions are nearly always short, but *Aucuba* and *Aconitum* are exceptional in this respect (*v.* Fig. 65).

(*c*) Prophase contraction of all sections of chromatids between two constrictions proceeds until the chromatid reaches the diameter

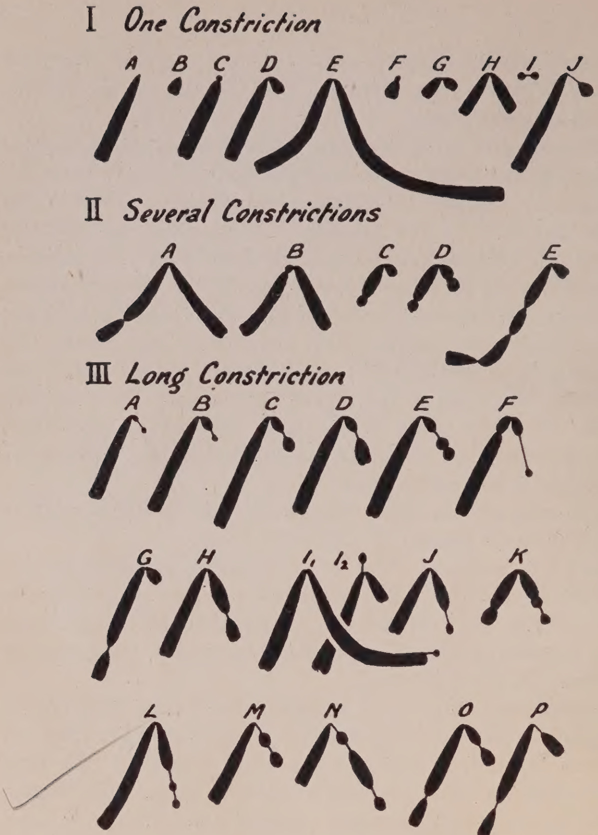

I One Constriction
A B C D E F G H I J
II Several Constrictions
A B C D E
III Long Constriction
A B C D E F
G H I₁ I₂ J K
L M N O P

FIG. 4.—DIAGRAM OF CHROMOSOME FORM AT MITOSIS

Metaphase chromosomes of plants and animals represented uniformly with the same diameter and with the two chromatids in the same line of vision at the constrictions, which are therefore represented by single threads. This is only constantly the case with polar views of the attachment constriction : in side views of this constriction the connection is double, the chromatids being seen side by side ; in polar or side views of other constrictions the connection is double or single according to the chance arrangement.

I. Chromosomes with a single constriction.

A. Terminal, *e.g.*, *Stenobothrus lineatus* (Janssens, 1924; Belar, 1928), *Drosophila melanogaster*, X-chromosome (Stern, 1929), *Sphæromyxa sabrazesi* (Belar, 1926 *b*).

B. Terminal, short chromosome, *e.g.*, *Drosophila melanogaster* fourth chromosome (Stern, 1929), *Yucca filamentosa* (Taylor, 1925 *b*). Many

Lepidoptera. *Cambarus* (Fasten, 1914), *cf.* Wilson. Many fungi: *Camarophyllus* (Bauch, 1926), *Saprolegnia* (Mäckel, 1928).

C. Sub-terminal (i) minor element spherical. *Fritillaria* and *Crepis* species (very common).

D. Sub-terminal (ii), *e.g.*, *Fritillaria, Ornithogalum, Tulipa, Crepis* species (very common).

E. Median or sub-median, *e.g.*, *Tradescantia virginiana* and *Fritillaria ruthenica* (D., 1929 *c*), *Aulacantha scolymantha, Euglypha* sp., *Monocystis magna, Salamandra maculosa* (*cf.* Belar, 1926 *b*).

F. Sub-terminal, short chromosome, *e.g.*, *Tradescantia fluminensis*, fragments of *Fritillaria imperialis* and *Tradescantia virginiana* (D., 1929 *c*).

G. Sub-median, short chromosome, *e.g.*, *Ornithogalum narbonense* (Delaunay, 1925, 1929), *Veltheimia viridiflora* (Taylor, 1925 *a*), *Muscari tenuiflorum* (Delaunay, 1926), *Commelina bengalensis* (D., 1929 *c*), *Lachenalia* spp. (Moffett, unpublished).

H. Sub-median, medium length chromosome, *e.g.*, second and third chromosomes of *Drosophila melanogaster* (Stern, 1929), *Crepis* spp. (Hollingshead, 1928), *Prunus* spp. (D., 1928).

I. Terminal, both chromatids spherical, very short chromosome as compared with the rest of the complement. *Muscari latifolium* (Delaunay, 1929).

J. Sub-terminal long constriction, *e.g.*, *Aconitum* spp. (*cf.* Fig. 65).

II. Chromosomes with several constrictions, all short.

A. Simple secondary constriction, *Hyacinthus orientalis* (D., 1926), *cf. Aucuba japonica* (Meurman, 1929), *Vicia Faba* (Sakamura, 1920).

B. " Intercalary trabant," *e.g.*, *Rhoeo discolor* (D., 1929 *c*). *Cf. Muscari polyanthum* and *M. pycnanthum* (Lewitsky and Tron, 1930) (?) *Cyrtanthus parviflorus* (Taylor, 1925 *a*).

C and D. *Muscari polyanthum* (Lewitsky and Tron, 1930), *Œnothera* spp. (D., 1931).

E. Multiple constriction, *e.g.*, *Fritillaria pudica* (D., unpublished).

III. Long secondary constrictions.

A. *Ranunculus acris* (Sorokin, 1927), *Crepis* spp. (Babcock and Navashin, 1930).

B. *Muscari longipes* (Delaunay, 1926), *Calochortus amabilis* (Newton, 1927), *Spironema fragrans* (D., 1929 *c*), *Crepis* spp. (Babcock and Navashin, 1930).

C. *Ornithogalum tenuifolium* (Delaunay, 1925), *Cyanotis zenonii* (D., unpublished) *cf. Lachenalia* spp. (Moffett).

D. *Ornithogalum narbonense* (Delaunay, 1925), *Crepis setosa* (Taylor, 1925 *b*).

E. *Ornithogalum nanum* (Delaunay, 1925).

F. *Bellevalia azurea*, *cf.* also *Muscari polyanthum* (Lewitsky and Tron, 1930).

G. *Fritillaria* spp. (Taylor, 1926; D., 1929 *c*, 1930 *c*).

H. *Crepis tectorum* (Hollingshead, 1928). *Fritillaria ruthenica* (D., 1929 *c*).

I_1. *Aloë saponaria* (Taylor, 1925 *b*), *Bellevalia romana* (D., 1926), *Tradescantia virginiana* and *Rhoeo discolor* (D., 1929 *c*), *Crepis pulchra* (Hollingshead).

I_2. Mutant form with lateral trabant in *Tradescantia* (D., 1929 *c*, Fig. 77; *cf.* Levan, 1932).

J. *Ribes aureum* (Meurman, 1928; D., 1929 *d*). *Rubus* spp. (Crane and D., 1928).

K. *Dahlia Merckii* (Lawrence, 1929), *Œnothera* spp. (D., 1929).

L and M. " Tandem " trabants. L. *Allium Cepa* (Taylor, 1926). M. *Aucuba japonica* (Meurman, 1929).

N. Intercalary trabant. *Solanum Lycopersicum* (D., unpublished). (*Cf.* Lewitsky and Benetskaia on *S. tuberosum*.) (*N.B.* This chromosome has led to difficulties in counting the chromosomes in *Solanum*, *cf.* Winkler, 1916).

O. *Cyrtanthus parviflorus* (Taylor, 1925 *a*).

P. *Aconitum* spp. (Fig. 65).

characteristic of the race, unless it first reaches a spherical shape. When the whole chromatid, or any section of it, is less than a certain size, the characteristic breadth is not attained. In the first case we have the spherical type of chromosome found in many animals and in *Muscari latifolium* (Fig. 4 I). In the second case, merely a part of the chromosome is narrower than the rest (Fig. 4 I C). But it often happens that such a part is terminal and is separated by a long constriction from the main chromosome, for long constrictions are more frequent near the ends. We then have what is called a "satellite" or *trabant*. Occasionally this condition is found in a small section intercalated in the middle of the chromosome. We then have an "intercalary trabant" (Fig. 4 III N).*

(*d*) Where a number of constrictions occur in each chromosome the complement presents an appearance of some complexity. Extreme examples of this are seen in *Datura* and *Œnothera* (Lewitsky, 1931; D., 1931 *d*), and in the "tandem trabants" of *Allium* (Fig. 4).

(*e*) The only restriction observable in the free combination of various forms of constriction in different chromosomes is indicated by the rarity of forms with long constrictions separating two large limbs of a chromosome. Further, the long constrictions are commonest where the distal element is smallest, *i.e.*, in a trabant, Doubtless this is because in most organisms a long constriction would not be strong enough to stand the strain of the anaphase separation with a large element distal to it. Selection, therefore, has probably played some part in limiting the range of chromosome form.

Two obvious modifications of the chromosome structures described might be expected, *viz.*, branched structure and simple ring structure. Both have been seen to arise as mutations, and the reason for their not occurring normally is probably to be found in their instability. The branched structure was seen in a chromosome of a new type in a pollen grain mitosis of *Tradescantia virginiana* (D., 1929 *c*), and consisted in a trabant attached laterally next to the attachment constriction of a medianly constricted chromosome (Fig. 4 III I_2).* The ring structure was found in a plant of *Crepis tectorum* (Navashin, 1930). Its behaviour is instructive in three respects: (i) it varies in degree of linear contraction to give sometimes the appearance of a disc instead of a ring. Its structure, therefore, interferes with its assumption of a spiral form, as might be expected (*v.* Ch. X). (ii) It is distributed irregularly at anaphase, for nuclei differ in the number of chromosomes present. Its own irregularity also possibly affects other chromosomes. (iii) Two ring chromosomes are sometimes found interlocked at metaphase (Fig. 5), presumably through the two halves having been interlocked at a previous division. This means that when the chromosome divides it does not divide in any one plane determined by external conditions, but by random alignment of reduplicated particles, such that the two new threads in a ring chromosome may or may not be interlocked.

---

* The view here expressed that the trabant is distinguished from other parts of the chromosome by its small size (D., 1926) has been disputed by the Russian school (*cf.* Sorokin, 1927), who have endowed the trabant with special functions. The observation of intercalary as well as terminal trabants, however, leaves no doubt of their being determined merely by the position of constrictions.

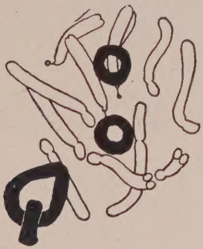


FIG. 5.—Metaphase of mitosis in root-tip of abnormal plant of *Crepis tectorum*, showing fifteen chromosomes instead of the normal eight. The four in black are the ring chromosomes, whose abnormal separation has led to their reduplication; two are interlocked. *Cf.* origin of polyploidy, Ch. III (from Navashin, 1930).

(iii) **In the Resting Stage: the Theory of Permanence.** The numbers, sizes, shapes and constrictions of the chromosomes appearing at mitosis are constant. In the nuclei of an individual or of a group of individuals descended by mitosis from a single nucleus, apart from such special accidents as will be considered later, the same " complement " is found. With sexual reproduction other changes may occur, but these are not common enough to interfere with the generalisation that each species has a characteristic chromosome outfit or " complement " seen at mitosis (*v.* Plate I). Apart, therefore, from such changes as are known to occur during division, the chromosome complement at mitosis is a constant property of the nucleus. This means that each chromosome that appears at the prophase of one mitosis corresponds exactly with a chromatid that entered into the nucleus at the preceding telophase in all its cytologically distinguishable properties except that it is double: it seems to have reproduced itself identically. It was on the assumption of this essential constancy of behaviour that Weisman predicted the universal occurrence of a reduction that would compensate for the addition that occurs when nuclei conjugate in fertilisation.

---

* This type of chromosome has recently been found in somatic nuclei in *Allium* (Levan, 1932) and *Alstroemeria* (La Cour, unpublished). It has also been inferred in *Drosophila* (*v.* Chs. III and X).

The correspondence may be attributed to one of two conditions. Either it is due to conditions that are external to the chromosomes in the same sense as a correspondence in form between the walls of two cells is due to conditions external to the cell-walls, or it is due to conditions inherent in the chromosomes themselves. This would mean that the chromosomes, or essential parts of them, are, unlike the cell-wall, *permanent* structures, arising, like the nucleus as a whole, the cell as a whole, or the organism as a whole, only from pre-existing structures of the same kind. This hypothesis, which is expressed by saying that the chromosomes have the same *individuality* as nuclei, cells and organisms, was verified by the work of Boveri (1892–1909) on *Ascaris*. Boveri found embryos that developed from eggs in which only one polar body had been formed, owing to the failure of separation of two nuclei at the second meiotic division. Clearly the original failure of the separation would give egg nuclei with two chromosomes instead of one. Fertilised by a sperm with one chromosome the first segmentation nuclei should have three chromosomes. All the nuclei of embryos arising in this way (still recognisable from the single degenerated polar body) had three chromosomes at mitosis.

Thus, if it is assumed that external conditions determine the number of chromosomes, it must also be assumed in this case that these conditions are permanently altered by an accident of separation which, on the individuality hypothesis, would lead directly and simply to the observed results.

This type of observation has been multiplied in recent years, so that any other hypothesis than the simple one of individuality and permanence would now be preposterous. Abnormal chromosome numbers have been discovered in relation to so many investigations that they must be separately considered in their special categories. All these observations are compatible with the doctrine of permanence, for these reasons: first, such differences as are observed can be understood in every instance as the result of changes that have been directly observed, or on other grounds inferred, in the individual chromosome or in the genetic properties of the nucleus as a whole. Secondly, the changes that take place are always irreversible in their effect on the chromosome complement and in the correlated effect on the organism as a whole, except through the reversal of the accident or change which is assumed to be directly responsible for the change in the complement on the hypothesis of permanence (*cf.* Buxton and D., 1932).

Now, if the constant structure of the chromosome complement is due to the inherent properties of the chromosomes, it may be supposed to be maintained in one of two ways. Each of the successive particles or chromomeres may have a specific affinity for the particles on either side of it, which causes it to enter into the same combination at successive mitoses. The changes in arrangement that will later be described show that this is not so. Alternatively, the essential linear structure of the chromosome thread seen at prophase may be retained during the resting stage. This idea of the continuous existence of the chromosome we owe in the first instance to Rabl (1885). It has been a matter of dispute ever since, and three different views are held with regard to the evidence.

Some consider that it is possible to trace the structure of the mitotic chromosomes through the resting stage from one division to the next by observations of appropriately treated nuclei. The results of staining the nucleus vary according to the fixative used and especially its *p*H. With certain combinations, *e.g.*, Navashin's solution and gentian violet, in roots of many plants, the nucleus appears optically empty. This is true even of early prophase, when structures of known significance can ordinarily be observed by other methods. By special treatment it has been possible in some plants to show a structure in the resting nucleus (Martens, 1928; Sharp, 1929; Kauffmann, 1931 *et alii*). It is said that in the spiral thread constituting the metaphase chromosome two substances may then be distinguished: a staining or "chromatic" substance and a non-staining or "achromatic" substance. The chromatic substance appears as a thread which is known as the "chromonema," and is alleged to have a continuous existence during the resting stage. The threads branch and anastomose so strangely that they can only be said to be recognisable as "chromonemata" (or to be characteristic artefacts representing these structures) to the eye of faith—the faith required being a belief that structures having the same staining reaction at different stages of mitosis necessarily have an organic relationship whatever the treatment to which they have been subjected. This is the belief that has already endowed the nucleolus with varied functions. There is no evidence for it. By salting out a structureless protein-water system the protein is concentrated in anastomosing threads of just the kind described, and this is probably what these investigators have been doing. It is interesting also to notice that those who undertake such delicate observations either arrive at no definite conclusion on the cardinal and relatively elementary question of the moment at which the chromosome-thread divides (Sharp, 1929) or disagree with observers approaching the question from other points of view in considering it already divided at telophase (Kauffmann, 1931).

Another kind of attempt to examine resting-stage structure consists in studies of "pro-chromosomes." These are bodies in the resting nucleus which stain darkly and are believed to be permanent structures representing the chromosomes. Kuhn (1929) has shown, in *Thalictrum*, *Phaseolus*, and *Capparis*, that they are to be regarded as parts of the chromosomes which have not yet gone into the resting condition. They disappear before the next division of the nucleus. It must therefore be admitted that direct observations of structure in the resting nucleus have so far failed.

An opposite point of view is taken by those who consider that the chromosomes cannot be individually represented by any structure in the resting nucleus. Schaede (1925–31) finds that the living nucleus, at least when " young," is optically homogeneous or granular, and considers this to be consistent with the view that no threadlike structure is present. The granular structure that is sometimes found might be given by an optical section of a coil of threads, but it certainly does not always correspond to such a coil, because, as Belar points out (1928, Fig. 5), the granulation is coarser the slower and more inefficient the fixation. Micro-dissection work has similarly suggested that the nucleus has no permanent structure and that its contents are " liquid " *in vivo* (Chambers, 1924). But failure to detect structure by these methods is not conclusive (*cf.* Heilbrunn, 1928). The structure that is sought is without analogy on a larger scale or in other materials.

The direct evidence of structure, whether positive from treated cells or negative from living cells, is therefore unreliable. This is a problem that must be resolved by more indirect methods of inference, and these, as we shall see, leave no doubt as to the essential conditions. The different kinds of evidence are so numerous that only selected instances can be considered here.

(i) The classical example was described by Boveri (1909), again in *Ascaris*. He showed that each of the several types of relative arrangement of the chromosomes seen at the beginning of a division in a young embryo corresponded exactly to one of the several types seen at the end of the previous division. Parts of the chromosomes, therefore, reappeared in just those parts of the nuclei where they had disappeared.

The same kind of evidence, but yet more striking, is afforded by the observations of Belar on *Aggregata* (1925, 1926). Here, owing to the rapid succession of divisions in the sporozoite, the longer chromosomes remain entangled at the ends at telophase (*v. supra*). They reappear entangled at the next prophase, and after two or three divisions the entanglement seen is precisely such as would have been expected had there been no resting stages. Similarly, Belar (1929 *b*) showed in living mitosis in the staminal hairs of *Tradescantia* that the polarised arrangement of the chromosomes corresponded at prophase with that seen in the preceding telophase. Finally the recognition of a spiral arrangement at prophase corresponding with that seen at telophase shows the persistence of the chromosome structure during the resting stage (*v.* spiral structure,

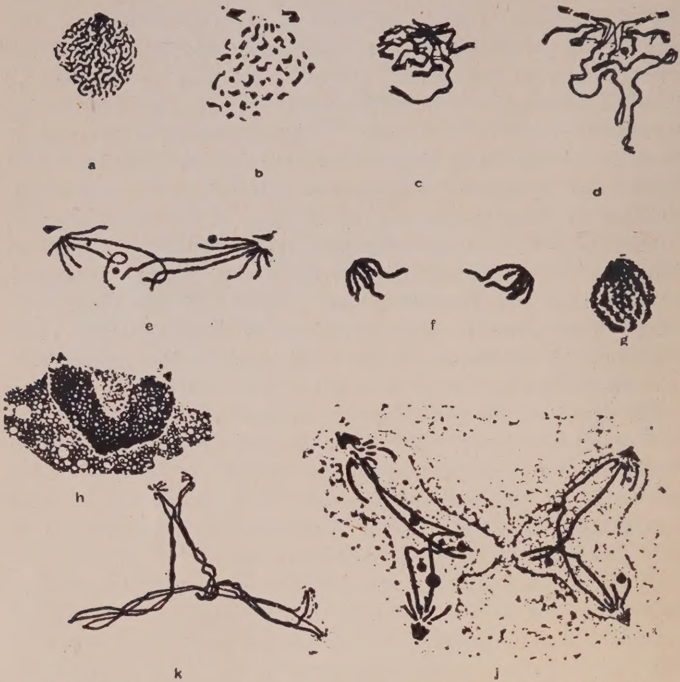


FIG. 6.—Mitosis in the spore-forming stage in *Aggregata eberthi* (Coccidia). a. Prophase. b. Early metaphase. c, d. Anaphase. e, f. Contraction of chromosomes at late anaphase. g. Telophase. h. A resting stage following failure of separation of the two bodies of chromosomes at the previous mitosis. j. Anaphase of mitosis following such a resting stage. k. Another anaphase showing further entanglement of the two long chromosomes after a rapid succession of divisions (from Belar, 1926).

especially Taylor, 1931; de Winiwarter, 1931). These observations show that the resting stage does not interfere with the structure and relationship even of the constituent parts of chromosomes. The chromosomes are not merely permanent but immobile. The description as a "resting stage" is mechanically and morphologically correct.

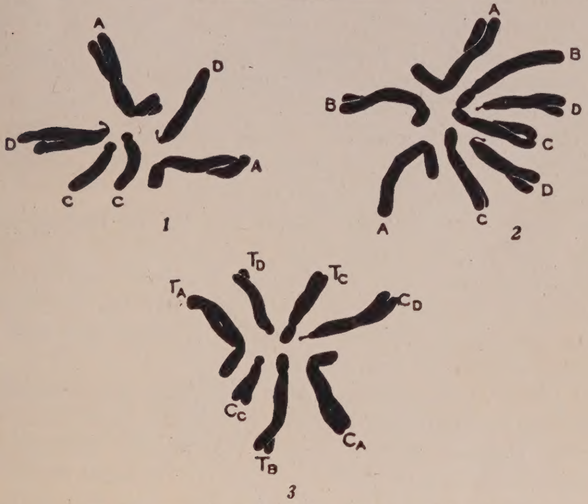


Fig. 7.—Mitotic metaphase: 1. in *Crepis capillaris* ($2n = 6$); 2. in *C. tectorum* ($2n = 8$); 3. in the hybrid between them ($2n = 7$). The chromosome types are marked with letters. Note that the D chromosome of *C. tectorum* shows no trabant in the hybrid. × 2300 (from Hollingshead, 1930; *cf.* Navashin, 1927).

(ii) Another kind of evidence consists in the demonstration of the separate existence of the chromosomes during the resting stage. This evidence is less decisive, because it may be held that such separation is only possible where the resting stage is short and therefore not a complete resting stage. For example, in the pre-meiotic resting stage of the spermatocytes (Wenrich, 1916, on *Phrynotettix*, Reuter, 1930, on *Alydus*, *et alii*) and in the early segmentation divisions of the fertilised egg (Heberer on *Cyclops*, 1925; Smith on *Cryptobranchus*, 1929) the chromosomes remain in distinct vesicles during the resting stage, from which they reappear at the ensuing prophase. In the spermatocytes of Orthoptera one chromosome (the sex chromosome) is more condensed than its neighbours and stains more deeply, so that it can be distinguished from the others throughout the resting stage. Similarly, in spermatozoa, even *in vivo*, it is sometimes possible to see the individual chromosomes and actually distinguish between those having different numbers (Mülsow, 1912, on *Ancyracanthus;* Meves, 1915, on *Filaria; v.* male gametes). Kater (1926) thinks it possible to distinguish the separate compartments in which the chromosomes lie during the resting stage in root tip nuclei.

(iii) Nemec (1929) was able to show that the reticular appearance of the fixed nucleus corresponded to a definite structure, for he found that this reticulum was definitely changed, lacerated, by the expulsion of the nucleolus in centrifuging and the shape of the nucleus was not immediately restored as it would have been if it had been structurally homogeneous.

(iv) Finally, a more elaborate kind of evidence is provided by the comparison of chromosome forms in hybrids with those found in the parents. Hybrids between species with clearly distinguishable complements have been studied in *Crepis*. It is found that each of the chromosome types of the parental species reappears, so that no two chromosomes are alike (Fig. 7, Hollingshead, 1930; Navashin, 1927). The constancy was not maintained in the second generation, for special reasons which do not concern the present problem (*v.* Ch. X). This kind of evidence is afforded also by the observations of Avery (1929) on other hybrids of *Crepis*, Meurman on *Ribes* (1929), Skovsted (1929) on *Æsculus* (Fig. 66), and by some older work.

Conclusion. There are three possible views of the structure of the resting nucleus (taking them in a different order): (i) that it has no fixed inherent structure; (ii) that it has a fixed structure which can only be inferred from observations of the dividing or damaged nucleus; and (iii) that it has a structure which can be directly seen after appropriate treatment. The first view leaves the observations recorded above as a series of coincidences (continually increasing in later pages) which can only be explained as supernatural. The last view depends on observations which are equally compatible with a complete absence of structure. Both these views are on other grounds to be regarded as misinterpretations (*v.* Appendix I). We are therefore left with the second view (less directly inferred): the particles making up the essential structure of the chromosome retain during the resting stage the relationship they have during mitosis. The basis of constancy of the chromosomes is therefore to be found in the permanence of the *linear arrangement* of their characteristic constituents seen as a fine open thread at early prophase of mitosis and as a closely coiled spiral thread at metaphase. This conclusion is of the first importance in genetics. The old dictum, *omnis cellula e cellula*, may be extended to nuclei, to chromosomes and to the unit-particles making up the chromosome, cytologically known as chromomeres, genetically as genes. It is perhaps even truer to say that all genes arise from pre-existing genes than that all cells arise from pre-existing cells, in this sense that the gene is an older structure than the cell (*cf.* Ch. XVI).

(iv) **When do the Chromosomes Divide ?** An increasing number of observations of the best material shows the chromosomes as double threads at the earliest prophase of mitosis. It has often been contended that the chromosomes have already split at the anaphase or telophase for the next division (*e.g.*, McClung, 1927 ; Robertson, 1931 *a*). The evidence is valueless, for the reasons given in the first section of this chapter. The conclusion is also incompatible with three series of observations. (i) Spiral structure is found in anaphase chromosomes (Kuwada and Sugimoto, 1926), and the supposed split would then cut across the spiral. (ii) A split spiral is found at the prophase, and there should be two independent spirals side by side if the chromosomes were already longitudinally split at the preceding division (Kuwada, 1921). The split appearance, on the other hand, is well accounted for by the considerations given above. (iii) The chromosomes are always single at the earliest prophase of meiosis (Plate III). This follows a normal telophase. Division cannot, therefore, normally occur before the resting stage.

The permanent thread is thus double at prophase (except in meiosis) and single at telophase. The one change that it undergoes during the resting stage is that of longitudinal division, presumably following the reproduction by each permanent particle or chromomere of one like itself, and the absence of this division distinguishes the resting stage before meiosis (*cf.* Ch. XI).

It may be that the polar granule, or something essential to the spindle attachment, does not divide at the same time as the thread itself, and has not the property, which the chromatids have, of associating in pairs. The special properties of the point of attachment will be clearer from a study of meiosis (Chs. XI and XII).

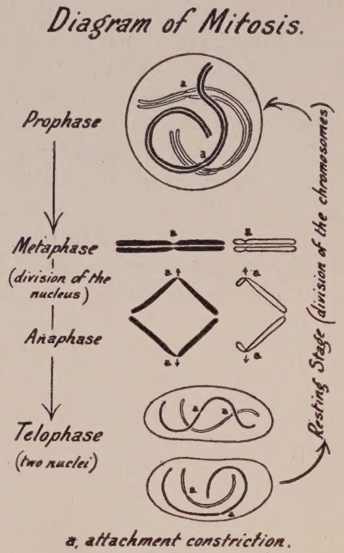


Diagram of Mitosis.
Prophase
Metaphase
(division of the nucleus)
Anaphase
Telophase
(two nuclei)
Resting Stage (division of the chromosomes)
a
a, attachment constriction.

FIG. 8.—Diagram to show the history of two chromosomes in the mitotic cycle.

Areas of endosperm, particularly after irradiation, may show the apparent results of "deficiency." This probably consists in the loss of a whole chromosome, since the recessive types of a group of linked factors may appear. Islands occur in which the dominants reappear. This may be explained as due to the failure of the chromosome carrying the dominants to divide, and its later recovery of this capacity (Stadler, 1930). Such an effect is most easily understood as the result of a single change, and it may be supposed that this change consists in injury to the spindle attachment which temporarily prevents its division and consequently the separation and redivision of the two chromatids. This may be compared with the observations of Bridges (1925, *a* and *b*) and Stern (1927) (*v.* pp. 56–58).

CHAPTER III

MITOSIS : THE VARIATION OF THE CHROMOSOMES

The Subordination of the Chromosomes to the Genotype—Numerical Variation of the Chromosomes—Polyploidy—Structural Variation of the Chromosomes—Fragmentation, Translocation and Other Changes—Comparative Morphology of the Chromosome Complement—The Sources of Variation.

> Per molto variare la natura è bella.
>
> Queen Elizabeth.

1. THE SUBORDINATION OF THE CHROMOSOMES TO THE GENOTYPE

(i) **The Chromosome Constants at Mitosis.** The chromosome complement at the metaphase shows certain properties which are characteristic of the individual and usually of the species. These *mitotic constants* are as follows :—

(i) The Bulk of the Chromosome. The constant appearance of chromosomes of characteristic bulk is attributed to the permanence of certain materials arranged in a thread during the resting stage. The bulk of the individual chromosome, which is constant, must be determined directly by the length of this thread—at least under constant genetic conditions.

(ii) The Diameter of the Chromatid. This must evidently be a function of the degree of longitudinal contraction of the chromosome thread during prophase during the assumption of a spiral. Apparently this contraction never proceeds beyond the point at which the chromatid, or segment of a chromatid in a trabant, is spherical. Very short segments do not therefore attain the characteristic diameter for the species. In some Protista, in very rapid mitoses, the contraction does not reach its characteristic maximum for any of the chromosomes (*e.g.*,*Aggregata*, Dobell, 1925; Belar, 1926, *a* and *b*). The fact that the diameter of the different chromatids in any mitosis is uniform indicates a single, and therefore genetic, control over the degree of contraction.

(iii) The Length of the Chromosome. This must also be a function of contraction and thread length. Since contraction is constant for the race, length is constant for the individual chromosome.

(iv) THE CONSTRICTION OF THE CHROMOSOME. The potentiality for constriction is evidently a characteristic of the parts of the individual chromosome, since their position is fixed. The sharpness of any constriction, and therefore its appearance, must be modified by the degree of contraction.

(v) THE NUMBER OF CHROMOSOMES. The number of separate chromosomes in the complement is fixed, apart from special changes to be considered later.

(vi) THE POINT OF ATTACHMENT. Each chromosome has a single spindle attachment at a constriction of fixed position.

Considering these constants, we can see that there are some that can be taken as expressing the permanence of the thread which goes to make the metaphase chromosome. Thus the potentiality for a constriction, especially the attachment constriction, and the *relative* length of the chromosomes must be directly determined by the permanent character of the individual chromosomes. This character is, however, consistent with variation in the appearance of the chromosomes in other respects. Especially the constant diameter of the chromosomes making up one complement suggests that this diameter has nothing to do with the permanent structure of the chromosomes, but is a racial, *i.e.*, a genetic character, and therefore subject to variation through genetic change (*cf.* Ch. I).

This means that the genetic properties of the organism, which are controlled by certain permanent materials (the genes) in the chromosome thread, themselves control, *within certain limits*, the form that this thread takes up at metaphase of mitosis. It is of the utmost importance in interpreting observations of chromosomes in terms of genetics to know what these limits are. We must therefore find out from a comparison of different species, races, mutants and hybrids what differences in their chromosomes can be attributed to changes in the permanent structure of the chromosomes affected (as described in the next section) and what differences are due to a different joint reaction of the genotype controlling the chromosomes as a whole. Both these kinds of difference will, on the chromosome theory of heredity, be due to changes in the arrangements or properties of genes, but the first will show in the part directly affected while the second, being due to gene mutation, will not be visible in direct effect at all, but will be seen by its altering the characteristic form or behaviour of the complement as a whole. Since both changes are genetic, the second kind will be distinguished as *genotypic*, for it takes effect through the action of the genotype as a unit (D., 1932 *a*).

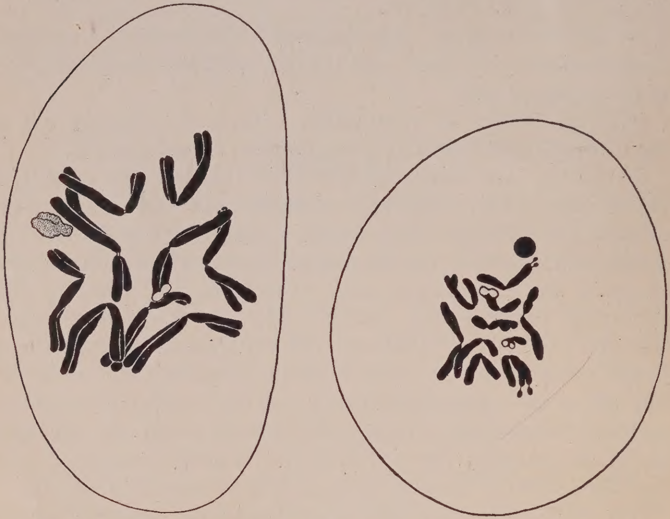


FIG. 9.—Mitotic metaphase in pollen grains from different flowers of *Tradescantia brevicaulis*, showing large and small chromosome types. A "degenerating" chromosome is seen in the left-hand plate, a persistent nucleolus in the right-hand one. *Cf.* Table 38, p. 231 (after D., 1929 *c*).

(ii) **Instances of Genotypic Control.** The following examples show the range of genotypic control seen at mitosis.

(i) CHROMOSOME SIZE. (*a*) *Tradescantia brevicaulis* is a triploid, apparently a hybrid between tetraploid *Tradescantia virginiana* with large chromosomes and a diploid relative with smaller chromosomes of proportionate diameter. It has chromosomes intermediate in length and width between those of its supposed parents. In the pollen grains of one bud of the plant studied the chromosomes were proportionately reduced to one-fifth and the resting nuclei to one-third of the normal size (Fig. 9). This was not associated with any change in the size of the cell (D., 1929 *c*, and unpublished).

(*b*) The chromosomes of *Vicia sativa* and *Vicia angustifolia* are smaller in the hybrid than in the parental species, at mitosis and meiosis (Sveshnikova, 1929, *a* and *b*).

(*c*) In *Sphærocarpus Donellii* the chromosomes as a whole and the cells are 1·7 times bigger in the female than in the male. This is largely accounted for by the presence in the female of the large *X* chromosome instead of the small *Y* chromosome, but partly also by the greater size of the other chromosomes. Apparently a genetic factor controlling chromosome size is correlated with sex in this species.

(*d*) In man and the rat the chromosomes are longer (and probably proportionately broader) in the male than in the female (Evans and Swezy, 1928, *cf.* Table 12).

(*e*) Similarly the chromosomes (or at least the *X* chromosome) are larger in the male *Melandrium* than in the female (Belar, 1927).

These changes in bulk are paralleled by the effects of differences of hydrogen-ion concentration on living chromosomes (Kuwada and Sakamura, 1926), and are probably to be ascribed to differences of dispersion of the permanent materials (genes) in the resting nucleus and in the chromosomes rather than to a different degree of proliferation of these materials.

(ii) CHROMOSOME WIDTH AND CONSTRICTION. (*a*) *Phragmatobia fuliginosa* occurs in two races, one with constantly greater linear contraction, and greater width of chromatid than the other at mitosis, and at meiosis (Seiler, 1925).

(*b*) Two individuals of *Melandrium album* have been found to have chromosomes constantly about one-third the normal length. They therefore resembled the normal meiotic chromosomes in shape (Breslawetz, 1929).

(*c*) In the third generation from the cross *Viola tricolor* by *V. Orphanidis*, a segregate appeared having longer and thinner chromosomes than the parental species, or indeed any other species, of *Viola*. This reduced contraction is correspondingly effective at both meiotic divisions. It must be contrasted with the *Matthiola* mutation in chromosome length (Ch. XIII), which only affects the first meiotic division (J. Clausen, 1931 *c*).

(*d*) The following table shows the total relative lengths of the chromosomes at mitosis in the haploid sets of three *Crepis* species and their first generation hybrids (Navashin, 1931 *b*; *cf.* Fig. 7).

TABLE 5

Lengths of Chromosomes in Species and their Hybrids

	Species.	Hybrids.	
		capillaris-neglecta.	*capillaris-tectorum.*
C. capillaris . .	108	126	109
C. tectorum . .	156	—	148
C. neglecta . .	97	83	—

The chromosomes of *capillaris* are longer, and those of *neglecta* shorter, in the hybrid than in the parent. It is also found that their bulk is the same, greater length meaning less width. It is to be assumed that the species are genetically different in regard to the control of chromosome contraction, while the genotype of the hybrid determines a uniform width in its chromosomes whatever their width in the parent from which they are derived.

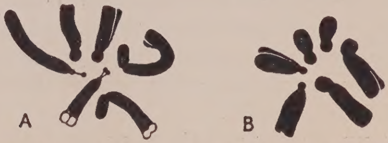


FIG. 10.—Mitotic metaphases in *Crepis capillaris*. A. Normal. B. In a root-tip that has been cooled before fixation. This change may be due to a difference in life or to a difference in the conditions of fixation. The difference is parallel to that found in different races of some species. × *ca.* 2000 (from Delaunay, 1930).

This difference has been imitated in *Crepis* by fixing under conditions of cold (Delaunay, 1929, *cf.* Fig. 10 ; *cf.* Appendix II).

(*e*) In hybrids of *Crepis capillaris* with *C. tectorum* and other species a trabant present in the *tectorum* parent is fused with the body of the chromosome, or rather the constriction separating the trabant is shortened to a minimum (Navashin, 1926, 1927; Hollingshead, 1930 *b* ; *v*. Fig. 7). This is probably associated with a slightly greater linear contraction of the *tectorum* chromosomes in the hybrid than in the parent. Conditions genotypically controlling the degree of contraction evidently determine how far the discontinuity in the chromosome thread shall express itself at metaphase.

(iii) CHROMOSOME AGGREGATION. (*a*) In certain species of *Ascaris* the fertilised egg contains a small number of large chromosomes. At the second and later segmentation divisions in those cells which are not going to give rise to germ cells, these large chromosomes break up into numerous small ones which remain independent in all the nuclei derived from them. The change is thus irreversible. In eggs that have been fertilised by two sperms and have divided into three or four cells at the first division instead of two, the number of nuclei with unfragmented nuclei at a later stage was correspondingly increased. Since it occurs in some species and not in others, this developmental property is evidently genotypically controlled, and the character may be

TABLE 6

Numbers of Chromosomes at Different Stages of the Life Cycle

	Somatic Mitoses.	Meiosis.	
		First Metaphase.	Second Metaphase.
Lymantria dispar *L. japonica* } ♂ and ♀ .	62	31	31
L. monacha } ♀ . . .	62	31	28
L. monacha } ♂ . . .	62	28	28
Phragmatobia fuliginosa : ♂ and ♀	56	28	28

described as the property of aggregation of the smaller chromosomes into larger ones, which is irreversible in the germ tract and reversible in the somatic nuclei, for the related species have the unaggregated condition in all their nuclei (Boveri, 1904).

(*b*) A reversible change, probably of the same kind, affects four small chromosomes in *Lymantria monacha*. They fuse to form a single chromosome at the second meiotic division in the female and at both divisions in the male, as counts show (Table 6).

Here a comparison with analogous species shows that the reversible change in one species has become a permanent one in its relatives, for the large aggregate chromosome is found in *Phragmatobia* constantly. The aggregation, it should be noted, has nothing to do with the ordinary pairing at meiosis, since it does not lead to segregation of the associated chromosomes to opposite poles (Seiler and Haniel, 1921).

A number of cases possibly corresponding to these are known. In *Philosamia* two pairs of chromosomes fuse temporarily at spermatogenesis (Dederer, 1928). The association of chromosomes in pairs in *Apis* and other Hymenoptera (*cf.* Nachtsheim, 1913) is probably also analogous to this fusion rather than to secondary pairing (*q.v.*).

(iv) CHROMOSOME DIMINUTION. (*a*) In *Ascaris*, at the same time as fragmentation, and in *Miastor* (Diptera), in the same circumstances, portions of the chromosome complement are left on the equatorial plate at anaphase. The portions lost are the distal ends of the fragmenting chromosomes in *Ascaris* and half the number of the chromosomes in *Miastor*. This change is necessarily irreversible (*Miastor*, Kahle, 1908; Hegner, 1914; *Ascaris lumbricoides*, Boveri, 1904).

(*b*) Two abnormalities of mitosis found in *Drosophila* are possibly analogous. Bridges (1925 *b*) found that the mutation Minute-*n* (a deficiency, lethal in the homozygous condition) had the effect of causing frequent elimination of the *X* chromosome which carries it. This effect shows strong susceptibility to changes in the environment. On two occasions the sister chromosomes making up the whole of a haploid set were eliminated along with the *X* chromosome, giving a patch of haploid tissue (Bridges, 1925 *c*). The effect is

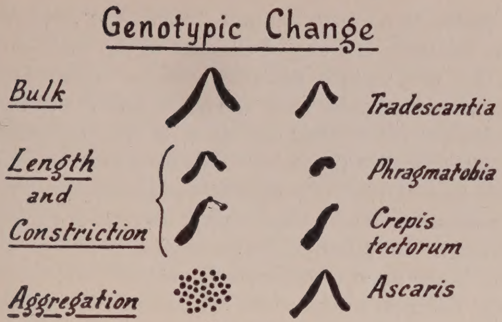

Genotypic Change
Bulk
Tradescantia
Length and Constriction
Phragmatobia
Crepis tectorum
Aggregation
Ascaris

FIG. 11.

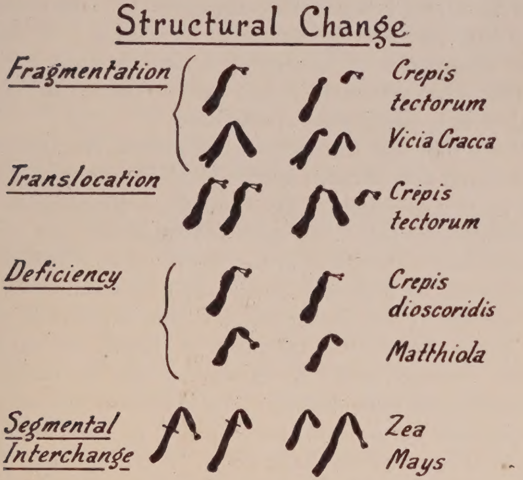

Structural Change
Fragmentation
Crepis tectorum
Vicia Cracca
Translocation
Crepis tectorum
Deficiency
Crepis dioscoridis
Matthiola
Segmental Interchange
Zea Mays

FIG. 12.

FIGS. 11 and 12.—Diagram to show the kinds of change produced genotypically and structurally in the chromosomes.

unexplained, but the ordinary elimination is essentially specific to the *X* chromosome, and since the determining mutation itself seems to be a structural change in this chromosome, it is easier to suppose that the elimination is structurally rather than genotypically produced.

Stern (1927) found two " minute " factors in *Drosophila* which led to the breakage and loss of the part of the third chromosome, in which they were located, and gave mosaics. One led to breakage at the spindle attachment only, the other (which was further from the attachment) led to breakage either at the attachment or at a point near the locus of the factor. Whole animals of this constitution would be inviable. The change was presumably irreversible.

(iii) **Conclusion.** These observations confirm the *a priori* views set out earlier. The relative form and behaviour of the chromosomes at mitosis in the same complement is evidently determined by the length and linear structure of the chromosome thread which exists permanently at division and in the resting nucleus. Under different genetical conditions, however, the same thread will behave differently in regard to (i) the bulk it assumes at metaphase ; (ii) the degree of linear contraction it undergoes during prophase ; (iii) the aggregation of its parts at all stages ; and (iv) the normal separation of its halves to opposite poles at anaphase.

It follows that the chromosome differences observed between individuals and also between species must be interpreted in terms of these genetic conditions. For example, a difference in the size of one chromosome may have much greater genetic and systematic importance than a difference in the size of all the chromosomes in the complement, for a general change may be determined by a much slighter change in one chromosome, if this happens to alter the genetic properties of the organism in regard to chromosome behaviour. Further, the individuality of the chromosomes is a purely mechanical individuality. The individual chromosome has no independent physiological control over its external form any more than it has over anything else. The chromosome is a unit statically as a structure seen at mitosis, dynamically as an organ of segregation ; physiologically, it is merely part of the genotype to which in many important properties it is subordinate. This subordination may be likened to the subordination of members of a legislature as individuals to the laws they enact as a body.

It is therefore necessary to distinguish in all chromosome behaviour between what is determined by the special properties of the individual particles and what is determined by the genetic reactions of the chromosomes as a whole, *i.e.*, by the genotype. This is particularly important for the analysis of the more complex phenomena of meiosis, where genotypic control plays an equally important part. These will be discussed later (Chs. X, XIII, XVI).

Note. The chromosomes of *Æsculus pavia* are about eight times as big as those of *Æ. Hippocastanum.* This distinction can scarcely be supposed to be one determined by a change in gene structure, especially since all the chromosomes are proportionately changed. Nor can it be supposed to be genetically determined, since it is retained in the hybrid, *Æ. carnea* (Skovsted, 1929, Fig. 66). It must therefore be due to a change in some permanent accessory material. The same is true of some lepidopteran hybrids (*cf.* Doncaster, 1920). A similar kind of difference has been described at meiosis between *Secale* and *Ægilops* (Berg, 1931), but the mitotic chromosomes show no size difference (*cf.* Emme, 1929, and Kagawa, 1929) and this interpretation cannot be accepted as it stands.

The physiological meaning of such an accessory material and its importance as compared with genotypic control in determining chromosome size cannot yet be decided (*cf.* Ch. XI).

2. NUMERICAL VARIATION OF THE CHROMOSOMES

(i) **Classification of Changes.** Reduplication of some of the chromosomes of a set beyond the normal diploid number is called *polysomy*, reduplication of the whole set so that the nucleus contains three, four or more sets is called *polyploidy*. The two combined give *secondary polyploidy* (D. and Moffett, 1930). Any of these can result from abnormalities of (i) mitosis, (ii) meiosis, (iii) fertilisation.

Polyploidy in itself involves no change in the numerical proportions of the chromosomes in the set; it is said to be a "balanced" variation. Polysomy, on the other hand, does involve such a change; it is said to be an "unbalanced variation," and has on this account an entirely distinct physiological effect (*v.* Ch. IX).

The reciprocal results from the same series of errors as those which give polyploidy and polysomy are found in cells or in whole organisms which lack either individual chromosomes through an error of mitosis (*e.g.*, *Zea Mays*, McClintock, 1929 *c*) or meiosis (*e.g.*,

TABLE 7

Types of Chromosome Constitution

Deficient Gamete $(x - 1)$.	Haploid (x).	Diploid $(2x)$.	Triploid $(3x)$.	Tetraploid $(4x)$.
A	*A*	*AA*	*AAA*	*AAAA*
B	*B*	*BB*	*BBB*	*BBBB*
C	*C*	*CC*	*CCC*	*CCCC*
—	*D*	*DD*	*DDD*	*DDDD*
E	*E*	*EE*	*EEE*	*EEEE*
Uvularia, Belling, 1925.	Normal Gamete.	Normal zygote. " Unreduced " gamete (*v.* Ch. XIII).	(*v.* Table 31).	(*v.* Table 31).

Monosomic Diploid $(2x - 1)$.	Trisomic Diploid $(2x + 1)$.		Tetrasomic Diploid $(2x + 2)$.	Doubly Trisomic Diploid $(2x + 1 + 1)$.
AA	*AAA* or	*AA*	*AAAA*	*AAA*
BB	*BB*	*BBB*	*BB*	*BBB*
CC	*CC*	*CC*	*CC*	*CC*
D—	*DD*	*DD*	*DD*	*DD*
EE	*EE*	*EE* etc.	*EE* etc.	*EE* etc.
Zea Mays, McClintock ; *Drosophila*, Bridges, 1916 ; Mohr, 1931.	*Œnothera* (no $2x + 2$), *Datura*, etc. (Tables 39–42).			*Œnothera*. *Datura*. *Solanum*.

Trisomic Tetraploid $(4x - 1)$.	Pentasomic Tetraploid $(4x + 1)$.	Doubly Hexasomic Tetraploid $(4x + 2 + 2)$.
AAAA	*AAAAA*	*AAAA AA*
BBBB	*BBBB*	*BBBB BB*
CCC	*CCCC*	*CCCC*
DDDD	*DDDD*	*DDDD*
EEEE etc.	*EEEE* etc.	*EEEE* etc.
Datura, Belling and Blakeslee, 1924. *Primula kewensis*, Newton and Pellew, 1929. *Biscutella lævigatus*, Manton, 1932. *Cf. Triticum vulgare* $(6x + 1)$, Kihara, 1921 ; Huskins, 1928.		Secondary polyploids, *e.g.*, *Dahlia Merckii*. Pomoideæ (*v.* Ch. VIII).

Haplo-IV in *Drosophila*, Plate VII, Fig. 14) or whole chromosome sets (*e.g.*, haploid parthenogenesis, *q.v.*).

The table explains the nomenclature of polyploids by examples from a type with a haploid set of five chromosomes (*A* to *E*), and shows the conventional formulæ in terms of the haploid number x.

Since a zygote usually receives two similar sets of chromosomes from its two parental gametes, their number is conventionally referred to as $2n$; where the chromosomes pair regularly at meiosis they therefore form n pairs. Now in a particular individual these $2n$ chromosomes may consist of three sets or four sets of chromosomes relative to its own parents or ancestors. In the present work, therefore, the " basic number " of this ancestral set is distinguished by the sign x. Thus in *Triticum vulgare* $2n = 42$ and $x = 7$, the somatic chromosome number is therefore hexaploid ($6x$). Similarly in a trisomic tetraploid form of *Primula kewensis* (where $x = 9$) $2n = 35$, and this number will be represented as $4x - 1$.

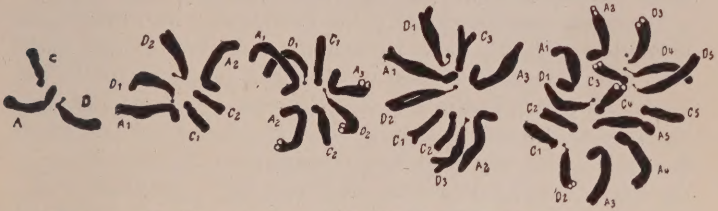


FIG. 13.—Mitotic metaphases in haploid (after Hollingshead, 1929), diploid, trisomic diploid, triploid and pentaploid (from Navashin, 1926) in *Crepis capillaris* ($x = 3$, chromosomes labelled A, C and D). × 1500.

When polyploid and polysomic cells or whole individuals arise in experiment they can be identified by four criteria : (i) The physiological properties of the organism, depending on the balance of the chromosomes. (ii) The number of the chromosomes. (iii) The morphology of the chromosomes. This test is applied in the study of mitosis, and is completely satisfactory in favourable material, *e.g.*, in *Crepis*, where each type of chromosome can be recognised (Fig. 13). (iv) The pairing of the corresponding chromosomes at meiosis (*q.v.*).

(ii) **Polyploidy.** Tetraploid nuclei arise from diploid in the somatic tissue of plants and animals, probably through failure of the two bodies of chromosomes to separate at the anaphase of a mitosis (*v.* somatic pairing, Ch. VIII). Such nuclei are normally found in certain specialised tissues of animals and very generally in some Hymenoptera. They have been observed amongst spermatocytes in the moth *Philosamia cynthia* (Dederer, 1928), and in *Drosophila* (Bridges, 1925 *a*). They are also usual in certain abnormal or degenerating tissues of plants, such as the galls produced by parasites (*Beta maritima*, Nemec, 1926) and the tapetal tissue surrounding the pollen mother-cells. Here tetraploid and octoploid nuclei are regularly found. Such aberrations may also be induced by special treatment, as in Boveri's experiments with echinoderm eggs, where the division of the centrosome was inhibited and a single nucleus reconstituted at the end of mitosis.

The callus tissue developed round wounds by some of the higher plants is particularly liable to such abnormalities. Double nuclei have been found in the callus of a haploid tomato by Koos and Lindstrom (1931), and in this way tetraploid, octoploid and other abnormal nuclei may arise in the diploid. Tetraploid (*4x*) plants first arose in this way in grafting experiments in *Solanum* (Winkler, 1916) and Crane (*cf.* Jørgensen and Crane, 1927 ; Jørgensen, 1928 ; Sansome, 1931) developed the method to produce tetraploids systematically. Usually about 6 per cent. of adventitious callus shoots are tetraploid in *S. Lycopersicum.* Poisoning and ill-treatment of various kinds have been used to induce doubling of the chromosome number in root-tips (*cf.* De Mol, 1921 ; Nemec, 1929).

Doubled nuclei having arisen with normal frequency probably develop with exceptional vigour in haploids which are often distorted and modified by the occurrence of diploid tissues with larger cells either as islands or as whole shoots (*cf.* Hollingshead, 1930 ; *v.* Ch. VIII). Thus amongst 110 root-tips of haploid *Crepis capillaris* there were 42 wholly diploid and 28 partly diploid, and one partly tetraploid. Amongst 82 root-tips of haploid *Nicotiana Tabacum*, 22 were wholly diploid and 8 partly diploid (Ruttle, 1928). *Datura* haploids, like those of *Crepis* (*cf.* Hollingshead, 1930 *a*) have yielded diploid shoots.

In tissues in which polyploid nuclei have arisen, these nuclei have been observed to divide by multipolar mitoses. A spindle is then formed with three or four poles, as in a doubly fertilised echinoderm egg, and the chromosomes are distributed at random to these poles. This has been found both where the polyploid cells were developed in galls and following chloralisation. The result is the production of nuclei with chromosome numbers once more reduced (Nemec, 1926, 1929). Whether this is the basis of variations such as the halving of the number in the tetraploid, observed by Winkler (1921) in *Solanum nigrum*, is doubtful, for equivalent halving is scarcely likely.

The chief occasion of polyploidy in plants and in many animals is the reunion, after separation, of nuclei in the male germinal cells at the last divisions before meiosis. This is known as syndiploidy. In some cases multinucleate cells may be formed without fusion (*e.g.*, in *Zea*). In most cases the fusion takes place after the pachytene stage of meiosis (*q.v.*), for the nucleus, although tetraploid, does not produce quadrivalents at metaphase in *Datura*, *Zea*, *Prunus*, or, as a rule, in *Brassica*. In *Prunus* and *Chrysanthemum* the abnormality is more far-reaching, for small supernumerary nuclei may be formed. This correlation of failure of formation of the cell-wall with failure of aggregation of the chromosomes into single nuclei is characteristic of extreme cases, for both processes depend upon the activity of the spindle.

The observations on animals and on *Brassica* and *Datura* show that the abnormality is often a racial, *i.e.*, a genetic, character. It has been more frequently discovered in hybrids, partly because it is more readily noticed in them, and partly because it is an undesirable character eliminated in species.

The following are some of the cases of syndiploidy recorded :—

TABLE 8

Instances of Syndiploïdy in Germinal Tissue

ANIMALS

Lacertilia, various species, Painter, 1914.
Iguanidæ, all species, Painter, 1921.
Gomphocerus maculatus (Orthoptera), Eisentraut, 1926.

PLANTS

Œnothera . . .	Geerts, 1909; Håkansson, 1927.
Lactuca . . .	Gates and Rees, 1921.
Zea Mays . . .	Randolph and McClintock, 1926. McClintock, 1929. Beadle, 1930 (recessive factor, asynaptic type, *v.* Ch. XIII).
Triticum compactum .	Gaines and Aase, 1926 (haploid plant).
Syringa . . .	Florin, 1926.
Raphanus × *Brassica* .	Karpechenko, 1927.
Nicotiana tabacum . .	Ruttle, 1928 (haploid plant).
Pyrus Malus . . .	Kobel, 1927. Nebel, 1929.
Triticum × *Ægilops* .	Kagawa, 1929 *a* (pentaploid).
Prunus avium vars. . .	D., 1930.
Brassica japonica . .	Fukushima, 1930 (one race only).
Datura Stramonium var. .	Blakeslee, 1930 (recessive factor).
Anthoxanthum odoratum .	Kattermann, 1931 (tetraploid).
Avena sativa . . .	Nishiyama, 1931 ($6x - 2$ plant).
Chrysanthemum ornatum .	Shimotomai, 1931.

There is evidence for somatic doubling in other tissues being also determined by a special racial propensity in some cases. In *Kniphofia Nelsonii* one plant had independent and repeated doubling in root and stem, giving tetraploid and octoploid tissue (Moffett, 1932). This is doubtless correlated with the spindle abnormalities found in the pollen mother-cells (Ch. XIII). Octoploid nuclei are also found in the abnormal race of *Datura*. In *Citrus limonum* tetraploid seedlings arise vegetatively in a regular proportion, probably through especially frequent doubling in nucellar tissue (Frost, 1925; *v.* nucellar embryony).

The third source of polyploidy in plants is from failure of reduction in the maturation in both male and female germ cells. This failure is particularly common at meiosis in hybrids, but may also be a racial character (*v.* Ch. XII). The distinction between this method of origin and the first, by somatic doubling, can often be made in a particular case because a somatic change will give a whole tetraploid region with diploid germ-cells, while diploid germ-cells will only arise sporadically by the second method (*cf.* Sansome, 1930; and Ch. VII).

Finally, tetraploidy may arise by natural apospory and artificial regeneration in ferns and mosses.

Tetraploid animal forms have appeared in experiment only in *Drosophila melanogaster.* In the females of this species Bridges has found tetraploid (and hexaploid) tissue in the ovary. This, giving diploid eggs, yields triploid offspring which in the second generation has given a few tetraploids producing diploid eggs (Morgan *et alii*, 1925). Polyploids are only known naturally in a few animal species. These are parthenogenetic in the tetraploid form when sexual in the diploid (*v.* p. 466). Polyploidy can be inferred in the hermaphrodite Mollusca and Annelida (*cf.* Ch. VIII).

This suggests that the rarity of tetraploid animal forms is due to the upset of the chromosome mechanism of sex differentiation, as has been found in *Empetrum* (Hagerup, 1927) where a diploid species is diœcious while its tetraploid relative is hermaphrodite. It may be thought, on the other hand, that the closed growth system of animals is responsible for the absence of polyploids, but, while this is a factor which will operate against their occurrence, it does not account for the complete absence of sexually reproducing polyploids (*cf.* Muller, 1925 *b*).

The nuclei of the endosperm in the flowering plants are triploid through the fusion of three nuclei, but such is not the origin of most triploid plants in experiment and in nature (*v.* fertilisation). One method of origin is by an abnormality in somatic mitosis in the haploid generation. Newton (1927) found nuclei at the third division of the embryo-sac with the diploid number of chromosomes, instead of the haploid, in many species of the Leiostemones section of *Tulipa*, of which this behaviour appears to be a characteristic. The doubling sometimes occurs regularly and presumably through the failure of anaphase separation at the division of one of the first two daughter nuclei in the embryo-sac (the second meiotic division). When it happens at the antipodal end it will result in the formation of endosperm with the tetraploid instead of the usual triploid number. When it happens, as it does exceptionally, at the egg-cell end, the embryo resulting from fertilisation will be triploid. This aberration therefore accounts for the occurrence of triploid forms and species in *Tulipa* and perhaps elsewhere in the Liliaceæ where non-hybrid triploids are common (*v.* pp. 120, 199).

Triploids are probably derived more often through failure of reduction at meiosis (*q.v.*) on one side, and the consequent fusion of reduced (*n*) and unreduced (*2n*) gametes. In this way triploids have been produced in *Ascaris* (Boveri), *Drosophila* (Bridges, 1921 *a*), and in *Pygæra* hybrid back-crosses (Federley, 1913, 1930). This method of origin is particularly frequent in the dicotyledons.

Finally triploids arise by hybridisation between diploids and tetraploids of the same species (*Œnothera, Primula, Zea, Datura*) or of another (*Rubus, Prunus, Fragaria, Avena, Triticum*) (*v.* Table 28D).

(iii) **Polysomy.** Polysomic forms arise in a diploid through two daughter chromosomes passing to the same pole at mitosis, or at meiosis. The first abnormality is doubtless stimulated by adverse external conditions, but disproportionately small chromosomes are especially liable to it (*v.* Section 4 (ii)). The same abnormality affects the ordinary members of the chromosome complement less frequently. Navashin (1930) has observed the two halves of one chromosome passing to one pole in the plant of *Crepis tectorum* with the ring-chromosome. In *Drosophila*, irregular division in this way is the cause of gynandromorphism when a female cell with two *X*-chromosomes gives a daughter cell with one *X*, which yields a male sector, and of " diminished mosaics " when a fourth chromosome is lost (Mohr, 1931 ; *cf.* Fig. 14).

The second abnormality has been shown to follow in meiosis : (*a*) failure of pairing ; (*b*) " non-disjunction " of paired chromosomes which then pass to the same pole ; (*c*) " non-disjunction " or irregular distribution of the components of a multivalent configuration in a polyploid or of a ring in a structural hybrid. The first of these cannot strictly be called non-disjunction, although this term is used by geneticists to cover the results of all three types of abnormality, when they cannot be directly identified.

True non-disjunction of simply paired chromosomes is rare except where these are disproportionate in size either to one another or to the rest of the complement, as with the paired fragments of

Tradescantia virginiana (D., 1929 *c*; *cf.* Wilson on *Metapodius*). Abnormalities from the other sources are common, and will be considered in relation to meiosis.

Non-disjunction and failure of pairing have been found with exceptional frequency in the progeny of X-rayed *Nicotiana Tabacum* (Goodspeed, 1929). The reason for this is probably to be sought not in structural change in the affected chromosomes, but in genetic changes such as are known to control the conditions of chromosome pairing at meiosis. These irregularities give rise to gametes with abnormal chromosome numbers.

In *Datura* trisomic plants appear spontaneously from diploids. They also arise by crossing diploid with triploid as in *Solanum*, *Crepis* and elsewhere (*v*. Ch. IX).

3. STRUCTURAL VARIATION OF THE CHROMOSOMES

(i) **Classification.** The permanence in "structure" of the chromosome complement is due, as we have seen, to the permanence in the linear order of a series of different particles, chromomeres or genes, according to the way their existence is inferred. Chromosomes may therefore be represented as of constitutions *abcdef, ghjklm, nopqrst,* and so on. All the conceivable variations in structure compatible with this linear arrangement of particles in separate threads have been observed or inferred both cytologically and genetically. Certain anomalous arrangements not compatible with this simple kind of structure have also been found.

They may be classified as follows, considering two chromosomes of one haploid set. (The other set may change in the same way, where the change is not lethal in the homozygous condition; or it may be normal, in which case the organism is a structural hybrid).

(i)	Original chromosomes	*abcdef, ghjklm*
(ii)	Fusion	*abcdefghjklm*
(iii)	Fragmentation	*abcdef, ghjk, lm*
(iv)	Translocation (from (iii) + (ii))	*abcdeflm, ghjk*
(v)	Deficiency or "deletion" (following (iii))	*abcdef, ghjk*
(vi)	Reduplication (recombining (i) and (iii))	*abcdef, ghjklm, lm*
(vii)	Reduplication (recombining (i) and (iv))	*abcdeflm, ghjklm*
(viii)	Interchange (or reciprocal translocation)	*abcdlm, ghjkef*
(ix)	Inversion	*abcdef, ghjkml*

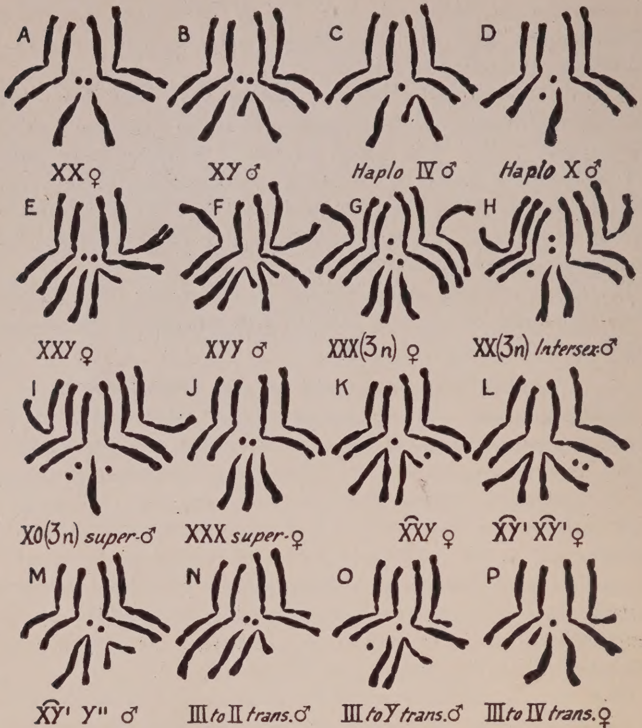

A
B
C
D
XX ♀
XY ♂
Haplo IV ♂
Haplo X ♂
E
F
G
H
XXY ♀
XYY ♂
XXX(3n) ♀
XX(3n) Intersex ♂
I
J
K
L
XO(3n) super-♂
XXX super-♀
X͡XY ♀
X͡Y' X͡Y' ♀
M
N
O
P
X͡Y' Y'' ♂
III to II trans. ♂
III to Y trans. ♂
III to IV trans. ♀

FIG. 14.—Diagram showing normal (A and B) and variant (C to P) chromosome complements of *Drosophila melanogaster*. Compiled from Bridges, 1916 (D, E, F), 1922 (G, H, I, J), 1927 (A, B), L. V. Morgan, 1925 (K), Stern, 1929 (L, M—alternative sex-mechanism), Muller and Painter, 1929 (N, O), and Dobzhansky, 1929 (P). Constrictions are emphasised. × *ca*. 9000.

D, E and K the products of primary non-disjunction. F of secondary non-disjunction. K of fusion. N, O, P of translocation. L and M of deletion with fusion. The structure of the chromosomes is otherwise constant. The XO male and the super-male and super-female forms are sterile, the first for mechanical reasons, the others for physiological reasons.

All these changes, save the last, have been inferred from the comparative study of the mitotic chromosomes (Fig. 12). New forms and numbers of chromosomes are found which can be simply ascribed to changes of these kinds. Observations on meiosis where the same kind of inference is used may be included with these, but the special inference of structural changes which depends on the principles of pairing at meiosis requires separate consideration (Chap. V).

TABLE 9

Classification of Observations giving Evidence of Structural Change

A. Fragmentation.

1. At mitosis in some cells, but not in others of the same diploid plant.

Crepis tectorum (*D* chromosome, Fig. 12). Navashin, 1931 *a*.

N.B. Some invalid observations in *Œnothera* (Lutz, 1914; Hance, 1916).

2. At meiosis in some cells, but not in others of the same plant.

Uvularia, (Belling, 1925).
Matthiola, (Lesley and Mann, 1924).
Tradescantia, (D., 1929 *c*).

N.B. Many invalid observations at anaphase owing to misinterpretation of bivalent separation or of nucleolar residues.

3. At the first post-meiotic (haploid) mitosis in some pollen grains, but not in others in the same plant.

Tradescantia spp. }
Rhœo discolor } (D., 1929 *c*). (Fig. 9).

4. At mitosis, or meiosis, in offspring of plants which had no fragments. This is usually reduplication as well.

Matthiola incana (Snowflake parent) (Lesley and Frost, 1928; Philp and Huskins, 1931).
Datura Stramonium (Belling, 1927; Blakeslee, 1930, 1931) (from X-ray treatment).
Digitalis mertonensis (new tetraploid F_4) (Buxton and D., 1932).
Nicotiana Tabacum ($4x - 1$) (J. Clausen, 1930, 1931).
Crepis capillaris × *C. aspera* (F_2, $3x$) (Navashin, 1927).*
C. capillaris × *C. tectorum* (F_2, $3x$) (Hollingshead, 1930 *b*).*

* Indicated by deficiency.

Solanum Lycopersicum ($2n + 1 + 1$ selfed) (Lesley and Lesley, 1929).

5. In individuals or races of unknown origin (compared with normal type).

(*a*) Appearing as a single change.
Vicia Cracca (Sveshnikova, 1927). (Fig. 12.)
Phragmatobia fuliginosa (Seiler and Haniel, 1921).

(*b*) Appearing with the probable reduplication of one product.
Metapodius and *Diabrotica* (Wilson, 1905, 1910).
Alydus (Reuter, 1930).
Solenobia (Seiler, 1925).
Secale cereale (Gotoh, 1924; Belling, 1925).
Zea Mays (Randolph, 1927).
Tradescantia bracteata and *T. virginiana* (D., 1929 *c*).
Fritillaria imperialis (D., 1929 *c*, 1930 *c*). (Fig. 15.)
Ranunculus acris (Langlet, 1928).
Crepis tectorum (Navashin, 1926).
Naias marina (Winge, 1927).
Primula spp. (Bruun, 1931).
Allium allegheniense (Levan, 1932).

(*c*) Appearing with loss of one product (part of one chromosome).
Matthiola incana (Philp and Huskins, 1931) (whole trabant).
Crepis dioscoridis (Navashin, 1926) (part of trabant, Fig. 12 and Plate I.)
Mus musculus (Painter, 1927).
Drosophila melanogaster (Stern, 1929) (part of *Y* chromosome).

B. Fusion,

1, 2, 3. None.

4. *Crepis tectorum*: (i) ring chromosome (Navashin, 1930 *a*, Fig. 5).
(ii) in X-rayed plant (Navashin, 1931 *c*).
Drosophila melanogaster (attached-*X*) (L. V. Morgan, 1922; *cf*. Anderson, 1925; and Rhoades, 1931).

5. *Crepis tectorum* (Navashin, 1926).

Hesperotettix viridis
H. speciosus
H. pratensis
Mermiria bivittata } (McClung, 1905, 1914, 1917, Fig. 37).

Jamaicana spp. (Woolsey, 1915).

C. Translocation.

1. *Crepis tectorum* (Navashin, 1931 *a*).

(i) Arm of *A* on to *A*.

(ii) Arm of *D* on to *D* (Fig. 12).

2. *Stenobothrus lineatus* (Belar, 1929 *a*) (from one chromosome to its partner ; observed in living cells at anaphase).

3. *Tradescantia brevicaulis* (D., 1929 *c*, branched chromosome).

4. *Drosophila melanogaster*.

(i) Attached *Y′* (Stern, 1929) (with loss of arm, *v*. Fig. 14).

(ii) Various new types from X-rayed parents (the segments transferred are usually terminal but occasionally interstitial) (Dobzhansky, 1931 ; Muller and Painter, 1929).

Crepis tectorum, natural seed of trisomic (Navashin, 1931 *a*).

5. (i) Indicated by shifting in position of attachment constriction.

Rumex acetosa (intersexual plant) (Ono, 1930 *b*).

Crepis pulchra
Pterotheca sancta } (Hollingshead and Babcock, 1930) (probably characteristic of races).

Crepis tectorum (Navashin, 1926, " novation ").

(ii) Indicated by the presence of reduplication or increase in the size of the chromosome.

Crepis fœtida (Hollingshead and Babcock, 1930).

Galtonia candicans
Muscari tenuifolium } (*cf*. Navashin, 1926.)

(iii) Indicated by presence of branched chromosome *Allium allegheniense* (Levan, 1932).

(*Cf*. list of unequal chromosomes at meiosis.)

D. Interchange.

1, 2, 3. None.

4. (Inferred from genetical behaviour).
Drosophila melanogaster (X-rayed) (Muller, 1930 *b*).

5. (Inferred from chromosome form at meiosis in a hybrid; *cf.* Interchange Heterozygotes).
Zea Mays (McClintock, 1931, Fig. 12).

E. Inversion and Reduplication.

5. (Inferred from behaviour at meiosis in hybrids).
Aucuba japonica (Meurman, 1929 *b*).
Tradescantia virginiana (D., 1929 *c*).

The relative importance of the different kinds of change occurring spontaneously has been shown in two species of *Crepis* from analysis of 6,000 plants by Navashin (1926) as follows :—

TABLE 10

Analysis of Variation in Crepis

	Crepis tectorum ($n = 4$).		*Crepis capillaris* ($n = 3$).	
Normal individuals		3,957		1,989
Numerical variants :				
$3x$	16		11	
$4x$	5		—	
$5x$	—		(1) *	
$2x + 1$	10			
$2x + 2$	4			
$2x + 3$	4			
Total		39		11
Structural variants :				
Fragmentation	3 †		—	
Translocation	1 ‡		—	
Total		4		—
Total		4,000		2,000

* Different series of observations.
† One was trisomic.
‡ Also showed fragmentation.

(ii) Time, Place and Action of Structural Changes. From these observations several definite conclusions can be reached in regard to when, where, and how structural changes arise, as follows :—

1. Structural changes occur in chromosomes both in the mitotic and in the meiotic phase. They probably occur during the resting stage, or, at meiosis, during the prophase (*v.* Ch. X, secondary changes and crossing over). The occurrence in mitotic nuclei is most clearly shown by Navashin's observations of chimæras in *Crepis* roots consisting of altered and unaltered cells. The occurrence at meiosis is most clearly shown by observations of new fragments both at the metaphase of the first meiotic division and at the first post-meiotic division in *Tradescantia*.

2. New structural types may fail to survive. Obviously a new fragment without a spindle attachment will not survive mitosis unless it develops a new one. Fragments of various sizes are found at the pollen grain mitosis in *Tradescantia virginiana*, degenerating (Fig. 9). It seems probable that these are ones incapable of developing an attachment. Others behave normally as new chromosomes, and since they are all the same size, about one-tenth the length of a normal chromosome, it seems probable that the capacity for developing the attachment is then conditioned by size, a view which would account for the constant size of the fragments in this and other genera (*e.g.*, *Fritillaria* and *Ranunculus*). On this view it would seem that the capacity for developing an attachment is latent in all chromatin. If this is so, the remarkable constancy of attachments remains a puzzling problem.

Except for such observations of the first post-meiotic division, it is only possible to see those new structural types which have survived many mitoses. These show a great range of form, but certain other restrictions are evident. Thus fusion only occurs between new fragments and old chromosomes (as in translocation) or between whole chromosomes which have a terminal spindle attachment. Fusion then occurs at the spindle attachment (*e.g.*, in McClung's observations on the Acrididæ). Here again the fusions which occur may be at random and those that are seen may be the selected survivors. Again also the spindle attachment plays a decisive part.

It seems that if the two fused chromosomes have two attachments these must coincide.

3. Once the new structural type has survived the test of mitosis it is potentially as permanent as the chromosomes of the normal complement. But it often happens that in its size it is less well adapted than these to the conditions of mitosis or meiosis. The problem of its adaptation to meiosis will be considered later (Ch. V). In some species an enormous range of size is found in the chromosomes of the normal complement (*v.* Section 4 (ii)), and great constancy is sometimes also found in the number of fragments in an old clone. Thus in a *Tradescantia* plant with 5 fragments, 4 and 6 were found exceptionally while in a *Fritillaria imperialis* plant with

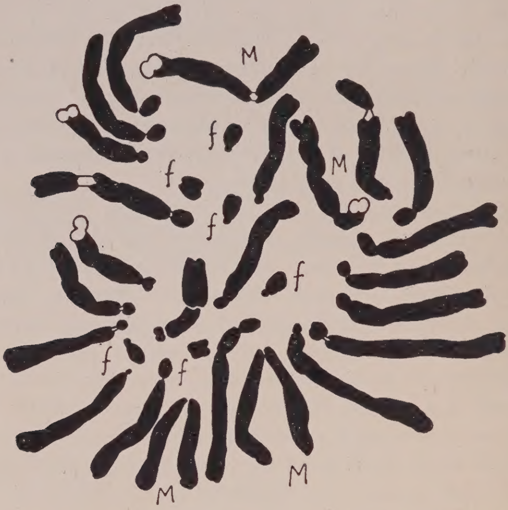


FIG. 15.—Mitotic metaphase in polar view in a clone of *Fritillaria imperialis* with six fragments ($2n = 24 + 6ff$). These are probably present along with the unfragmented sister chromosomes of those from which they are derived and are therefore reduplications. The chromosomes have been spread out in drawing; those with median attachment constriction are marked M. *Cf.* p. 80 and Fig. 25. × 2200 (from D., 1930 *c*).

6 fragments, 12 were found in an anther, evidently owing to both halves of each of the 6 going to the same pole in a mitosis, but otherwise the number was constant. In other species, behaviour is much less regular. In a group of *Ranunculus a cris* plants, probably of one clone that must originally have had six fragments, Langlet found 252 divisions with the following fragment frequencies:—

No. of fragments .	3	4	5	6	7	8	9	10
No. of mitoses .	1	21	40	148	23	14	1	3

Similarly in *Nicotiana* the frequent loss of a fragment having an abnormal effect on flower colour gave patches of normal colour in the abnormal (*cf.* Blakeslee, 1928, on *Datura*).

Thus mitosis in some species seems to be better adapted to deal with a wide range of size of chromosomes than in others and a suitable mitotic mechanism is a second condition of the survival of new types of chromosomes.

4. The difference between natural changes and those produced by X-rays cannot yet be defined with certainty, as other than a mere difference of frequency (*cf.* Muller and Painter, Stadler, Timofeëff-Ressovsky). The changes produced by X-rays in *Drosophila* usually seem to consist in something more than a change in linear arrangement. The adjoining particles must be altered, for the new type is not usually viable in the homozygous state. These changes seem to occur entirely at random.

Natural changes, however, do not occur either in time or place with the randomness that was once supposed. Some occur with a definite frequency in particular individuals. Thus half-mutants in *Œnothera Lamarckiana* which are due to interchange occur once in 2,000 seedlings. The attached Y′ in *Drosophila* occurs once in 1,500 flies (Fig. 14). This predictable regularity in the occurrence of a particular change suggests a relationship with crossing-over, and these changes probably occur at meiosis (*v.* Chs. X and XIV).

Changes of this kind occur characteristically in hybrids and are found in the second generation (*cf. A4*). They may take the form of fragmentation as in the two triploid *Crepis* hybrids, each of which showed loss of one arm of one chromosome. Or they may not be visible cytologically, but only in the altered character of the organism (*cf.* tetraploid *Crepis* derivative, Ch. VII).

5. In changes occurring at mitosis, aberration from randomness is more obscure. Navashin finds particular plants of *Crepis tectorum* of abnormal constitution giving a high proportion of changes in somatic mitoses. Evidently this property is a genetic one. Possibly it may consist in having an abnormal prophase with some of the characters of meiosis.

6. Constrictions do not necessarily arise from structural changes, for new chromosomes derived from fusion do not always show the point of fusion in this way in *Drosophila* or *Crepis* (Navashin, 1930, *b*, *abd*, *c*). It has been inferred that structural change had occurred at a constriction in *Aucuba* (*v.* p. 321). Observations of the fusion of fragments with the whole chromosomes in *Tradescantia* (D., 1929 *c*) tend to the same conclusion, but are of doubtful validity.

Since every chromosome in its history must have undergone an indefinitely large number of structural changes, it is impossible to consider that all these leave a permanent constriction. In this regard the conclusion to be derived from Navashin's and Hollingshead's observations of the disappearance of a trabant is significant, for it shows that the persistence of constrictions is conditioned by genetic factors as well as structural factors. Further studies will perhaps show more clearly the relationship of these factors to the appearance and disappearance of constrictions.

7. It has usually been supposed that a simple linear arrangement is the only kind that can be produced by structural change, since that is the only kind found in the somatic chromosomes of mature organisms. Probably it is in fact the only one compatible with stable reproduction at meiosis and possibly also at mitosis. But in *Tradescantia brevicaulis,* in which many structural changes occur at meiosis, a branched structure, called an "interstitial trabant" (more properly a *lateral trabant*) was observed at the first post-meiotic division (in the pollen grain). Such a structure is presumably the result of exceptional lateral fusion (D., 1929 *c*, Fig. 71), and is probably disadvantageous, for such structures have only been found twice in the permanent complements of species (Ch. II).

The translocation of a piece of one chromosome on to the side of another, *lateral translocation*, giving a branched structure, has been inferred genetically in *Drosophila* (Bridges, 1923; Hamlett, 1926; Sturtevant; *cf.* Dobzhansky, 1931 *a* and Ch. X).

The occurrence of more complex modifications of linear arrangement is suggested by the associated group of properties of certain unstable X-ray mutants in *Drosophila* found by Muller. The possibility of a branched or looped structure arising must be considered, especially in view of Navashin's observation of the ring-chromosome in *Crepis*.

8. The more detailed analysis of these changes will be made in examining the behaviour of structural hybrids at meiosis, and the survival of new types will be considered in relation to qualitative differentiation and balance (Ch. IX). It is from these considerations that the value of the observations of the fifth category, which are necessarily less conclusive than the others, may be understood, and the kinds of change effective in distinguishing species may be inferred.

4. THE COMPARATIVE MORPHOLOGY OF THE CHROMOSOME COMPLEMENT

(i) Specific. In the previous section comparison has been made of sister-cells, sister-individuals and sister-races. It may now be extended to sister-species and genera. The more distant the relatives compared, the less certain are the grounds of inference, but it will be seen that the relationships of species and genera can often be expressed conveniently in terms of the changes inferred from the study of smaller groups. It will also be seen later that more detailed study at meiosis bears out these conjectures in many instances.

In the first place our knowledge of polyploidy within the species suggests that when groups of species have chromosome numbers in a series of multiples of a common "basic number" and the chromosomes are of similar form, these species are probably derived from forms with this basic number by polyploidy (Winge, 1917). The application of this inference will be considered later in detail (Ch. VIII).

Structural changes may be inferred with some certainty from a

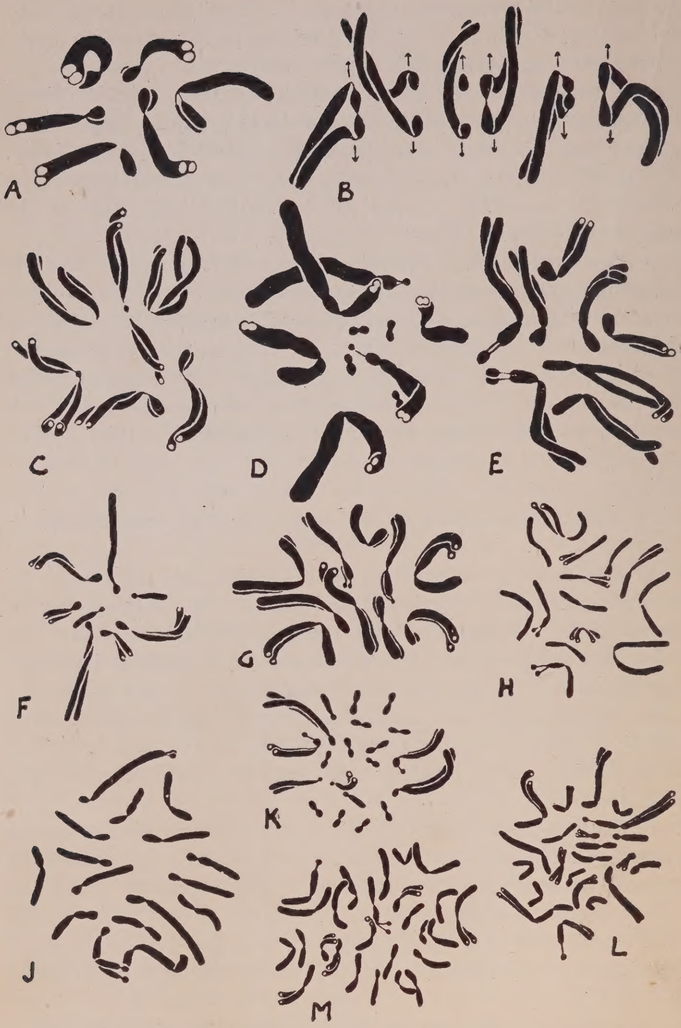

A
B
C
D
E
F
G
H
J
K
L
M

FIG. 16.—Mitotic chromosomes from root-tips of *Crocus* species. A, *C. Aucheri*, $2n = 6$. B, the same in side view of early anaphase. C, *C. graveolens*, $2n = 6$. D, *C. hyemalis*, $2n = 6 + 4ff$. E, *C. aureus*, $2n = 8$. F, *C. zonatus*, $2n = 8$. G, *C. stellaris*, $2n = 10$. H, *C. Hueffelianus*, $2n = 14$. J, *C. hadriaticus*, $2n = 16$. K, *C. karduchorum*, $2n = 20$. L, *C. corsicus*, $2n = 22$. M, *C. Imperati*, $2n = 26$. × 3700 (reproduced by kind permission of Mr. K. Mather).

Note.—C is early metaphase with the limbs of the chromosomes separate ; D is full metaphase with the limbs joined throughout their length. In B, arrows indicate the points of attachment at which the daughter-chromosomes begin to separate.

detailed comparison of chromosome form within genera and larger groups. Thus the chromosome complements within *Fritillaria* and the Acrididæ may be represented diagrammatically as follows (*V*, a long chromosome with median attachment ; *I*, a short chromosome with terminal or sub-terminal attachment).

Fritillaria (Figs. 15, 25, and) :									
F. ruthenica ($n = 9$) . .	V	V	V	V	V	I	I	I	I
F. imperialis ($n = 12$) *F. Meleagris* ($n = 12$) and six other species .	V	V	II	II	II	I	I	I	I
F. pudica ($n = 13$) . .	V	II	II	II	II	I	I	I	I
Acrididæ (females) :									
Stenobothrus *Chorthippus* *Chloëaltis* ($n = 9$) (Figs. 21–24) . .	V	V	V	I	I	I	I	I	I
Other genera ($n = 12$) . .	II	II	II	I	I	I	I	I	I

The direction of the changes suggested by this comparison necessarily cannot be settled by direct evidence. But the fact that the number 12 is constant in both the groups concerned, apart from the types given here with other numbers, suggests that these are derived from original forms with 12 chromosomes. Thus *F. ruthenica* and *Stenobothrus* are derived from ancestral forms by fusion, *F. pudica* by fragmentation.

A comparison of *Circotettix* with other Tettigidæ (Carothers, 1917, 1921 ; Helwig, 1929), of *Nicotiana alata* and *N. Langsdorffii* ($n = 9$, Kostoff, 1929) with other species ($n = 12$), of *Cardamine pratensis* with other species (Lawrence, 1931 *d*), of *Orgya thyellina* with *O. antiqua* (Cretschmar, 1928), and of various species of *Gryllus* (Ohmachi, 1930), indicates likewise fragmentation or fusion in the ancestry of these forms.

More complex changes, such as inversion and interchange, necessarily cannot be inferred from a comparison of mitosis in different species. They will be considered in relation to meiosis. But another method that may be mentioned here does show their occurrence. Comparison of the linkage groups which correspond with the different members of the haploid complement show inversion and other structural differences between races of *Drosophila* species, *e.g.*, in *D. melanogaster* (Morgan, 19), and in *D. obscura* (Koller, 1932). The same differences are found when different species are compared (Sturtevant and Plunkett, 1926; Sturtevant, 1929; Koller, 1932 *b*; *cf.* Ch. X).

When larger groups are considered a more generalised effect is seen. Thus in the ninety-four species of the Lepidoptera examined the greatest number of species is found with thirty-one chromosomes, and the frequency with other numbers diminishes regularly with increasing remoteness from thirty-one. This indicates, as Beliajeff (1930) points out, that the group has arisen from ancestral forms with this number. The variation in number has arisen by random fragmentation and fusion. The fragmentation and fusion account for certain differences in size of the chromosomes also, but not for more than a small part.

Dasychira pudibunda ($n = 87$), may be supposed to be derived by fragmentation from a *Lymantria*-like type with thirty-one chromosomes, for while most of the chromosomes are reduced in size, three pairs remain thirty or forty times the bulk of the rest.

On the other hand, where two species in the same family like *Spilosoma lubricipeda* and *Miltochrista miniata* have the same chromosome number and the chromosomes correspond in size-variation in each, but are throughout forty times larger in one species than in the other, probably genotypic control of chromosome size is responsible for the difference (*cf.* Beliajeff, 1930; D., 1932 *a*). *A fortiori* when between two species in the same family (Droseraceæ), there is difference of size in the proportion of a thousand to one, genotypic control of the difference is to be inferred (Table 12).

Structural changes in themselves have no necessary genetic effect, but they may condition a later genetic differentiation between species. We therefore find every relationship between structural and numerical and genotypic differences in the chromosomes on the one hand and systematic differences on the other, as follows :—

(i) The absence of readily detectable differences within large groups such as the gymnosperms—all of which have twelve haploid chromosomes except *Ephedra*, *Cupressus*, and perhaps *Cycas*—and the Acrididæ (except three genera); or the absence of all differences except polyploidy (*e.g.*, the Pomoideæ).

(ii) The occurrence of differences between genera of an order while the genera are themselves fairly uniform, *e.g.*, *Antirrhinum*, *Orchis* (*cf.* Tischler, 1928 *b*), *Ribes* (Meurman, 1929), *Prunus* (apart from polyploidy, D., 1930 *a*).

(iii) The occurrence of differences between sections of a large genus, *e.g.*, *Primula* (Bruun, 1930).

(iv) The occurrence of differences between all the species of a genus, *e.g.*, *Drosophila* (Metz), *Fritillaria*, *Tulipa*, *Crepis*, *Tradescantia*, *Muscari*, *Vicia* (and polyploidy in nearly all large angiosperm genera except *Antirrhinum*, *Ribes* and *Orchis*). (*Cf.* also McClung on *Mecostethus*, 1914, and D. on *Fritillaria*, 1930 *d*, with regard to differences peculiar to meiosis, *q.v.*)

(v) The occurrence of differences between geographical races or sub-species (*v.* Table 36).

(vi) The occurrence of differences between forms not recognisably distinct (*v.* Table 36, structural differences in some Orthoptera and polyploidy in *Silene*, Blackburn, 1928 ; and numerical variation in *Viola canina*, Clausen, 1931).

A comparison of the mitotic chromosomes of different forms is therefore of little value in placing them systematically unless we know the type of variation that prevails in the groups in question. If the forms have different chromosome numbers they are probably intersterile or yield sterile hybrids, a fact which the systematist may or may not take into consideration.

(ii) **General.** We now see the whole capacity for variation in the chromosome complement as it is shown to us at mitosis. The chromosomes are subject to two kinds of change : change governed directly by the activities of the part affected, and change governed by the reaction of the genotype as a whole, which usually has a uniform effect on the whole chromosome complement, although it is probably determined by a gene mutation which is itself invisible and strictly local in origin. The first is described as structural or numerical change according as it affects the internal arrangement, the structure, of a chromosome or the number of different chromosomes present. The second is described as genotypic change. When the chromosome complements of living organisms as a whole are compared, their variation is found to be such as can be described in terms of these two kinds of change.

The time has not yet come when their relative importance can be accurately assessed except in considering small groups of species. An internal and external comparison of the chromosome complements, however, indicates the part played by the two kinds of change. Differences within a chromosome complement indicate solely the range of structural change. Differences in the diameter of the chromosomes in different species indicate solely the range of genotypic change.

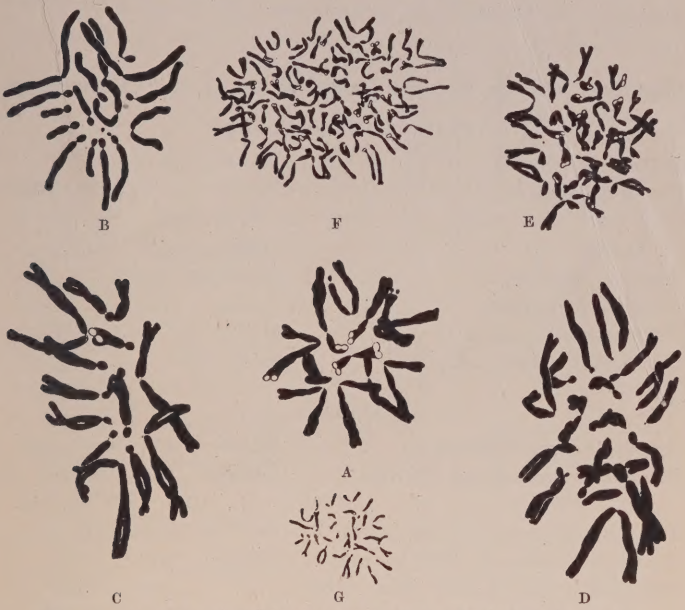


FIG. 17.—Variation found in the chromosome complement in species of a natural group, the Tradescantieæ. A. *Rhœo discolor*, $2n = 12$. B. *Cyanotis zenonii*, $2n = 16$ (by fragmentation). C. *Spironema fragrans*, $2n = 12$ (by loss of parts). D. *Zebrina pendula*, $2n = 24$ (by polyploidy). E. *Coleotrype natalensis*, $2n = 36$. F. *Commelina cœlestis*, $2n = 90$ (by polyploidy and fragmentation). G. *Cyanotis somaliensis*, $2n = 28$ (by fragmentation). F and G show reduced chromosome width. G shows reduced bulk, × 1800 (from D., 1929 *c*, and unpublished).

Most complements are uniform in the size of their members, which do not vary over a range of more than two to one. Exceptionally a much higher range of variation is found, reaching a maximum of 500 : 1 in the domestic turkey, *Meleagris* (Werner, 1931).

TABLE II

Organisms with an Extreme Range of Size in the Chromosomes

PLANTS (Monocotyledons)

Eucomis bicolor	Müller, 1912.
Yucca filamentosa	Taylor, 1925 *c*; Morinaga *et al.*, 1929.
Y. flaccida	O'Mara, 1931.
Muscari latifolium	Delaunay, 1926.
Uvularia grandiflora	Belling, 1926.
Fourcroya altissima et al.	Heitz, 1926.
Ornithogalum pyramidale et al.	Heitz, 1926.

ANIMALS

Aggregata eberthi (Sporozoa)	Dobell, 1925; Belar, 1926.
Drosophila melanogaster (Diptera)	Bridges, 1927; Morgan *et al.*, 1925. (See Fig. 14.)
Tettigonia albifrons (Locustidæ)	de Winiwarter, 1931.
Dasychira pudibunda (Lepidoptera)	Beliajeff, 1930.
Schistocerca paranensis (and other South American Acrididæ)	Saez, 1930.
Vipera aspis (Reptilia)	Matthey, 1929, 1931.
Eumeces latiscutatus (Reptilia)	Nakamura, 1931.
Meleagris gallopavo (and other Galliformes and Anseriformes)	*Cf.* Werner, 1931.

In other species the small chromosomes in the complements are variable in number, unessential to the species, and probably the result of recent fragmentation, as already described.

To turn to the comparison of different species, the lowest chromosome numbers are found in the nematode *Ascaris megalocephala*, which has two races, one with one haploid chromosome, the other with two; and in the Agaricaceæ (Wakayama, 1930), where species with two as their haploid number occur. In the flowering plants, nine species are known which have three as their haploid number, *viz.*, *Crepis capillaris* (*cf.* Babcock

TABLE 12

Range in Size and Number of Chromosomes

	Diploid No. of Chromosomes ($2n$).	Approx. Breadth (2 Chromatids).	Approx. Length.	Author.
1. *Aulacantha scolymantha* (Radiolaria).	ca. 1600	1·0μ	ca. 20μ	*Cf.* Belar, 1926.
2. *Ascaris megalocephala univalens* (Nematoda):				
(i.) Germinal . .	2	0·7μ	20μ	Boveri, 1909.
(ii.) Somatic . .	ca. 50	0·5μ	0·5μ	
3. *Cambarus virilis* (Crustacea)	200	3μ	3μ	Fasten, 1914.
4. *Drosophila melanogaster* (Diptera).	8	0·3μ	2·5μ	Bridges, 1927.
5. *Stenobothrus parallelus* ♂ (Orthoptera).	17	0·6μ	13μ	D. and Dark, 1932.
6. *Homo sapiens* (Mammalia)	48	0·6μ	5·4μ ♂ 4·1μ ♀	Evans & Swezy 1928, 1930.
7. *Sphæromyxa sabrazesi* (Myxosporidia).	6	0·2μ	2μ	Belar, 1926 *b*.
8. *Saprolegnia mixta* (Phycomycetes).	22	0·4μ	0·4μ	Mäckel, 1928.
9. *Humaria rutilans* (Ascomycetes).	16	0·5μ	5μ	Fraser, 1908.
10. *Hyacinthus orientalis* (Monocotyledones).	16	2μ	21μ	D., 1926, Fig. 33.
11. *Prunus laurocerasus* (Dicotyledones-Rosaceæ).	176	0·3μ	2·5μ	Meurman, 1929.
12. *Œnothera biennis* (Dicotyledones-Onagraceæ)	14	0·3μ	2·5μ	D., 1931 *d*, Plate IV.
13. *Crepis capillaris* (Dicotyledones-Compositæ)	6	0·9μ	6μ	Navashin, 1926, Fig. 7.
14A. *Drosera capensis* (Dicotyledones-Droseraceæ).	40	0·3μ	1·0μ	Behre, 1929.
14B. *Drosophyllum lusitanicum* (Dicotyledones-Droseraceæ).	12	2μ	25μ	*Ibid.*

and Navashin, 1930), *Callitriche autumnalis* (Jørgensen, 1923), *Zacintha verrucosa* (Navashin, 1930), and six *Crocus* species (Mather, 1932). The Table (p. 85) shows the range in size and numbers found in living organisms. It will be seen that the approximate ranges found in the various constants, represented as proportions, are as follows :—

Breadth, $1 : 10$ . . (*Sphæromyxa : Hyacinthus*)
Length, $1 : 10^{1\cdot 7}$ . . (*Saprolegnia : Hyacinthus*)
Bulk :
  Chromosome, $1 : 10^{3}$. (*Drosera : Drosophyllum*)
  Complement, $1 : 10^{4\cdot 1}$. (*Saprolegnia : Aulacantha*)
Number, $1 : 10^{3}$ . . (*Ascaris : Aulacantha*)

It is clear that such great differences in structure and number demand the assumption of both structural and genotypic change (especially when they are found within a single order). Their significance will appear more fully in considering meiosis and in the detailed examination of the relationships of chromosomes in related species.

CHAPTER IV

MEIOSIS IN DIPLOIDS AND POLYPLOIDS

Introduction—Outline of Meiosis—Meiosis in Diploids—Meiosis in Polyploids—Forms of Bivalents and Multivalents at Metaphase—Separation at Anaphase—Conclusion—The Conditions of Chromosome Pairing.

1. INTRODUCTION

> There must be a form of nuclear division in which the ancestral germ plasms contained in the nucleus are distributed to the daughter-nuclei in such a way that each of them receives only half the number contained in the original nucleus.
>
> WEISMANN, 1887.

STUDIES of fertilisation between 1870 and 1875 showed that the process consisted essentially in the union of the nuclei of the fusing germ cells (O. Hertwig). Studies of mitosis during the succeeding years showed that at every observed division of the nucleus or mitosis there was a division of its constituent elements, the chromosomes, into equal halves. These elements were constant in appearance, and therefore they were, as later work has abundantly shown, " permanent " structures.

It follows that, in the history of the nucleus from one generation to the next, wherever fertilisation occurs, there must also be some compensating process. Addition must be set off by *reduction*. This conclusion was arrived at by Weismann in 1887, although at that time the nature of the reduction was only slightly indicated by observations of germ-cell formation on the female side. Weismann noted that in certain parthenogenetic organisms only one polar body was extruded instead of two as in sexual eggs. He thought, therefore, that the division which yielded the second polar body was a " reducing division "—a conclusion that was sound in a certain sense. He further concluded that a similar reduction would be found in male germ-cell formation.

Weismann's induction has been verified universally: wherever there is fertilisation there is also reduction, or, as we shall call it, *meiosis.* The course of this verification has been beset with many difficulties, which will later be considered in detail. They have been discussed at length by several authors (Wilson, 1925; Belar, 1928; Reuter, 1930; D., 1931; *v.* Ch. XI, and Appendix I).

We may now define meiosis by its superficial phenomena as *the occurrence of two divisions of a nucleus accompanied by one division of its chromosomes.* It results in the production of four nuclei, each of which has half the number of chromosomes of the mother-nucleus, provided that their distribution has been regular.

From the principles set out in the first chapter, it will be clear that the occurrence of one form of nuclear division instead of another at a particular point in the development of the organism is an example of differentiation—in time, in the Protista, and in time and place, in the higher organisms. This differentiation being a racial characteristic must be genetically determined, although its origin is too remote for its exact conditions to be reconstructed. Organisms do occur, however, in which the reverse change has taken place, and meiosis has been more or less completely replaced by one or two mitoses. These cases show that the two forms of division are distinguished by a simple physiological difference which is controlled by the genetic properties of the organism. The nature of this difference and of this control will be considered later in relation to the theory of meiosis, of apomixis, and of the evolution of genetic systems.

2. OUTLINE OF MEIOSIS

The following sketch shows the succession of events in meiosis, as they occur in the simplest clear examples, *e.g.*, pollen mother-cells of diploid species of *Tulipa.* The process is described in more definite terms than were originally possible (Newton, 1927). Alternative nomenclature will be found in the glossary.

I. First Division. (*a*) *Leptotene.* The chromosomes appear in the nucleus in their diploid number as single threads. Each has an uneven granular structure which gives it the appearance of a string of unequal beads, unequally strung together. The beads are the *chromomeres.* The threads are disposed freely in the nucleus.

(*b*) *Zygotene.* The chromosomes come together in pairs,

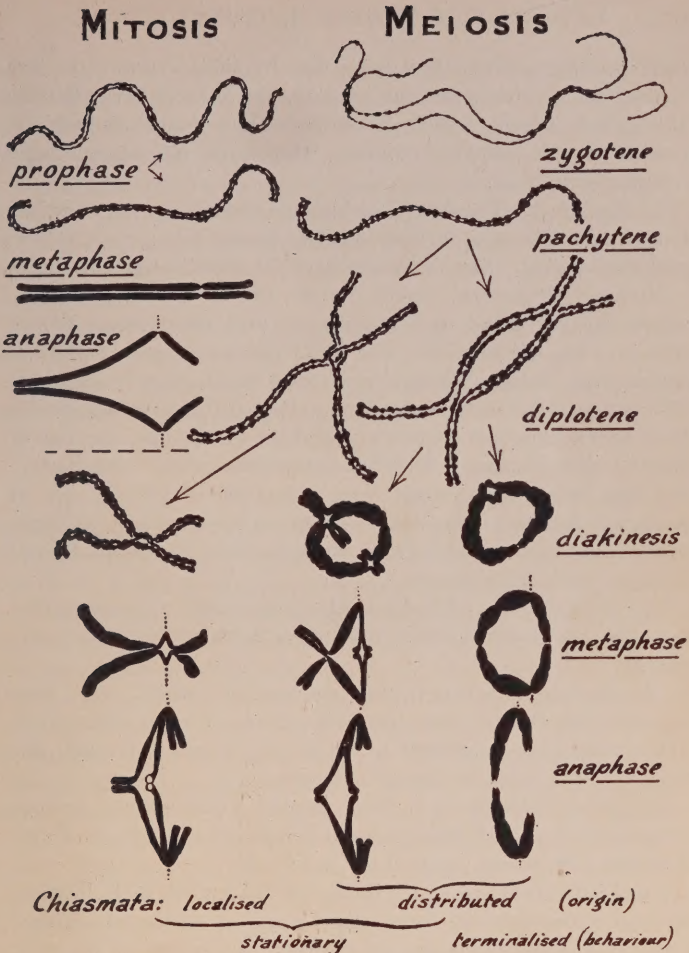

MITOSIS
MEIOSIS
zygotene
prophase
pachytene
metaphase
anaphase
diplotene
diakinesis
metaphase
anaphase
Chiasmata: localised
distributed
(origin)
stationary
terminalised (behaviour)

FIG. 18.—Diagram showing the history of one chromosome at mitosis and, for comparison, that of two pairing chromosomes at the first division of meiosis. These may follow one of three types of behaviour shown, according to the place of origin of the chiasmata and the amount of movement that they undergo (*cf.* Table 14). Note that the chromosomes reach the same degree of contraction between diplotene and diakinesis that they have at the mitotic metaphase.

corresponding chromomeres lying side by side. They come into contact at various points at random, the association extending along their length until it is complete, and double threads are present in the haploid number. Meanwhile the chromosomes contract lengthwise.

(*c*) *Pachytene.* The double or bivalent threads contract further, but remain otherwise without visible change for a more or less prolonged period. Signs may appear of the thread being quadruple.

(*d*) *Early Diplotene.* Splits appear in the bivalent threads, which are now found to be quadruple, each chromosome having split into two chromatids. The splits therefore separate pairs of chromatids. When they meet it is found that they have separated different pairs from among the four, so that at the points of meeting there are exchanges of partner amongst the chromatids, one, two or more in each bivalent. These exchanges are called " chiasmata," and are believed to result from crossing-over (*cf.* Ch. X) at pachytene between the chromatids derived from opposite partners, so that the two chromatids that remain together are always derived from the same chromosome.

(*e*) *Late Diplotene.* The bivalent chromosomes contract further until they are as short as the chromosomes at metaphase of a somatic mitosis.

(*f*) *Diakinesis.* Lengthwise contraction, which has been associated with lateral expansion since zygotene, reaches a maximum. The chromosomes continue to be evenly disposed through the nucleus. The nucleolar material disappears.

(*g*) (*First*) *Metaphase.* The paired chromosomes arrange themselves evenly on the equatorial plane in the spindle, and with their two attachment constrictions in its axis.

(*h*) (*First*) *Anaphase.* The four chromatids of each bivalent separate; the pairs of chromatids associated at the attachment constriction pass to the same pole, so that, in segments on the other side of a chiasma, chromatids that are paired must be separated.

(*i*) (*First*) *Telophase.* The chromosomes may form two daughter-nuclei at the poles and pass into a resting stage, the *interphase,* two separate cells being formed; or they may enter directly into the second division. In the first case they regain their normal mitotic length, in the second they retain their special contraction. The two daughter-nuclei each have the haploid number of chromosomes, but, since these are already divided, they have the diploid number of chromatids as in a mitotic telophase.

II. SECOND DIVISION. (*j*) (*Second*) *Metaphase.* At an early stage the two chromatids are widely separated—more so than in any somatic mitosis. They are then held together only at their attachment constrictions. Later stages have a purely mitotic character.

(*k*) (*Second*) *Anaphase.* The chromosomes are distributed as at an ordinary mitosis.

(*l*) (*Second*) *Telophase.* Four daughter-nuclei are formed, each receiving the haploid number of chromatids.

3. MEIOSIS IN DIPLOIDS

(i) **The Pairing of Chromosomes.** The prophase of meiosis begins after a resting stage which may be short or almost entirely omitted, so that the chromosomes which appear can be traced directly to telophase chromosomes whose individuality has never been even entirely lost. In the spermatogenesis of certain Orthoptera and Hemiptera, for example, the nucleus continues divided into as many compartments as there are somatic chromosomes until the prophase chromosomes appear (Wenrich, 1916, *Phrynotettix* ; Reuter, 1930, *Alydus* ; Chickering, 1927, *Belostoma*, etc. *Cf.* Ch. II). One chromosome comes from each compartment. It consists of a series of darkly staining granules, the chromomeres, of unequal sizes lying at unequal distances in a lightly staining thread (Plate III, Fig. 18). Both the granules and the thread are single so far as observation can show. In favourable material of some animals the threads can be counted from their attachment granules and shown to be present in the diploid number, as in somatic mitoses (Gelei, 1921 ; Janssens, 1924). This stage with separate single undivided threads is called the leptotene stage.

The chromosome threads may remain freely distributed in the cell, as in most of the higher plants, or they may gradually orientate themselves so that one or both ends of each thread lie towards one side of the nucleus (near the centrosome where one is present).

They are then said to be polarised, and as long as they remain so, that is, until pachytene, they present the appearance to which the name " bouquet " stage is given (Digby on *Osmunda*, 1919 ; Gelei on *Dendrocœlum*, 1921 ; Janssens on *Mecostethus* and *Stenobothrus*, 1924 ; Belar on *Actinophrys*, 1926 ; Kihara on *Rumex*, 1927 *a* ; Belar on *Tradescantia*, 1929 *b*). [For " synizesis " or collapse, *v.* Appendix I].

The single threads soon begin to associate in pairs side by side. If they are freely distributed in the nucleus, their association takes place at random, *i.e.*, in different parts at the same time. If they are polarised they usually associate first at their attachment constrictions, whether these are median or terminal (Wenrich, 1916, 1917), and the association passes along the chromosomes fairly regularly.

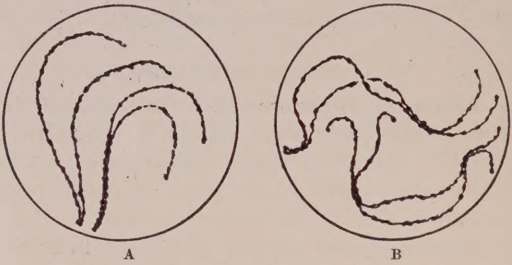


FIG. 19.—Diagram to show the difference between the method of pairing at zygotene with and without polarisation. A, as in *Stenobothrus* ; B, as in *Tulipa*.

The bouquet stage has been regarded as a possible characteristic of chromosome pairing (Gelei, 1921), especially on account of its absence in certain hybrids without pairing (*e.g.*, *Pygæra*, Federley 1913), and in certain parthenogenetic organisms without pairing (*e.g.*, *Aphis*, *v.* Baehr, 1912). Certainly the failure to observe its unfavourable material, such as many dicotyledons and Diptera, is inconclusive, but there can be no doubt of the absence of polarisation in many Lepidoptera (Seiler, 1914), and in some Liliaceæ (Newton, 1927 ; D., 1929 *b*). Polarisation may be regarded as an adaptation to secure regularity in pairing (*cf.* Gelei). It is bound to affect the distribution of pairing amongst the possible partners, whether segments in structural hybrids or whole chromosomes in polyploids (*v.* conditions of pairing).

From the first associations pairing extends along the threads until they are completely paired. The stage when this association is taking place is "zygotene"; the stage when it is complete is "pachytene." During pairing the chromosome threads gradually contract linearly as in ordinary mitosis. Each double thread is derived from two physically corresponding somatic chromosomes.

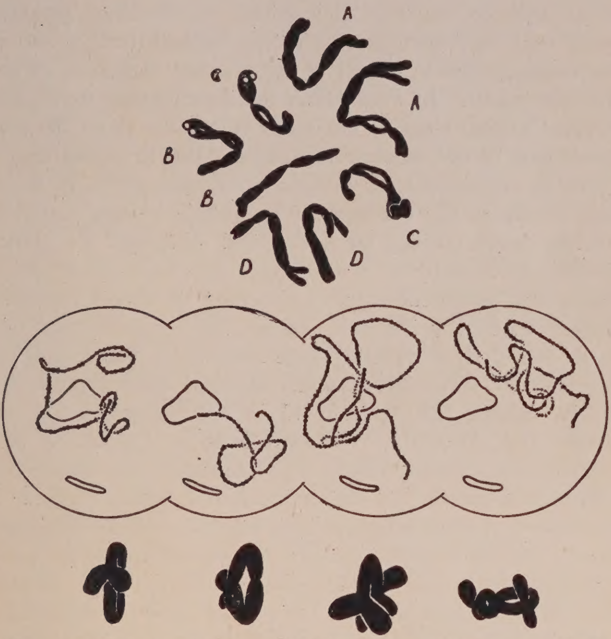


FIG. 20.—The chromosomes of *Bellevalia romana*. Top, at mitotic metaphase, $2n = 8$; four types, *A*, *B*, *C*, *D*. Middle, the four pairs of chromosomes at pachytene, drawn separately. Bottom, the four pairs at metaphase, each with two chiasmata except the rightmost, which has three. × 2,000 (reproduced by kind permission of Mr. S. O. S. Dark).

At leptotene the chromomeres are seen to be distributed at unequal distances along the chromosome thread, and the chromosomes as they pair are seen to correspond in regard to this structure. At pachytene successive granules are closely crowded along the thread. In *Phrynotettix magnus* Wenrich (1916) was able to represent each of the paired chromosomes separately, showing that they were present in the haploid number and that corresponding types in regard to the granular structure appeared in different nuclei. In *Phrynotettix* the chromosomes were already contracted at this stage to not more than three times the length characteristic of the somatic metaphase. But in plants they are still five or six times their mitotic metaphase length in the few species in which the contents of the whole nucleus have been separately drawn (Belling on *Lilium* and *Aloë*, 1928 *d*; Dark on *Bellevalia*, and Moffett on *Anemone*, 1932, Fig. 20, *v*. Ch. II, 4 (i)).

During the pachytene stage, which may be almost indefinitely prolonged without perceptible change, the nucleus may revert partially or entirely to a resting stage condition. This complication of development, which has naturally hindered the interpretation of successive stages, has been found in spermatogenesis in some organisms (*e.g.*, Hemiptera, Wilson, 1912; *cf*. Chickering, 1927), and in oögenesis in many more. In some species this change takes the form of a swelling of the chromosomes, which continue the normal course of development in their bloated condition (*Pristiurus*, Rückert). In other species the chromosomes disappear for a while and reappear again unchanged (*Gryllus*, Buchner, 1909). In others again (*Phanæus*, Hayden, 1925) the part of the nucleus containing the chromosomes condenses to one side to form a " karyosphere," in which the condensed pachytene chromosomes can be separately distinguished. These changes are inessential to meiosis; they appear to be determined by the special conditions of growth of the cell and the nucleus at this stage of the development of the animal egg. In many plants, such as *Hyacinthus*, similar changes occur which render the chromosomes incapable of satisfactory observation between pachytene and diakinesis.

(ii) The Separation of Chromosomes and the Origin of Chiasmata. The first evidence of further change is seen in the splitting of the double thread into two halves at different points. It is then found that each of the new threads is double. Each chromosome has divided into two chromatids. This stage is "diplotene."

The evidence of the best material (Janssens, 1924; Newton, 1927; Belar, 1928 *b*) is conclusive that the separating threads are double. How long the pachytene threads may have been quadruple is impossible to say, because the division cannot have been an instantaneous one (*v.* Ch. XI). The splits appear in the paired threads as a rule at several points and extend until they meet. It is then found that the splits separate different pairs of chromatids, for, at the point of meeting, the pairs change partners, giving, from one point of view, the appearance of a cross; hence the name "chiasma" is applied to the occurrence of this exchange (Janssens, 1909, 1924; Belling, 1928 *c*; D., 1930 *b*, 1931 *c*).

Chiasmata are formed as a rule in all paired chromosomes at this stage. But, as we shall see later, short chromosomes which have been paired at pachytene may in some cases be presumed to fall apart at this stage without the formation of chiasmata.

Chiasmata probably always arise in the first instance interstitially, *i.e.*, at some point between the ends of the chromosomes, not at the ends (*v.* Ch. XII). They vary in number from one to as many as thirteen in the pair of chromosomes or bivalent, but their range of variation is characteristic for each bivalent of an individual under constant conditions (*v.* Ch. XII and Plate VI).

This variation has certain characteristic properties in all organisms. Its curve is unimodal; the mode corresponds with the mean except where it approaches zero, when it is lower than the mean; the curve is a modification of a Poisson curve, in which the mean is favoured at the expense of the extremes. In other words, the occurrence of one chiasma operates against the occurrence of another in the same bivalent. This phenomenon will be referred to as *cytological interference*, and will be discussed in relation to the theory of crossing-over (*cf.* Haldane, 1931). The mean number of chiasmata per bivalent is approximately proportional to the length of the paired chromosomes. This is seen more clearly from quantitative records of chiasmata at a later stage, metaphase. At this stage in *Hyacinthus orientalis*, Stone and Mather (1932) find the

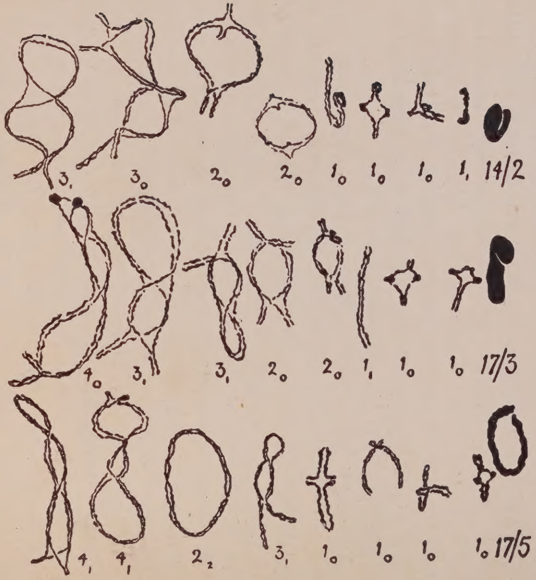

3_1 3_0 2_0 2_0 1_0 1_0 1_0 1_1 14/2
4_0 3_1 3_1 2_0 2_0 1_1 1_0 1_0 17/3
4_1 4_1 2_2 3_1 1_0 1_0 1_0 1_0 17/5

FIG. 21.

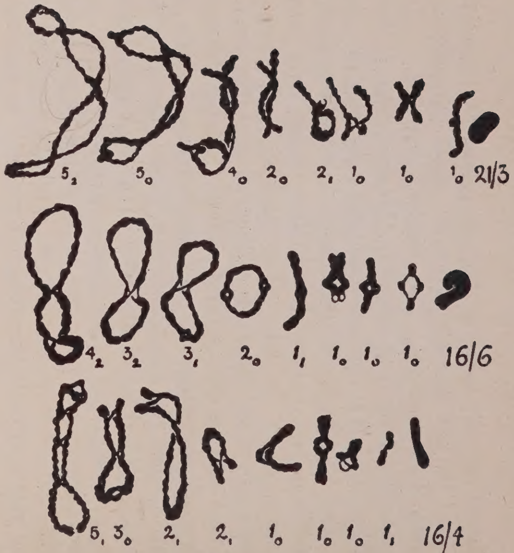

5_2 5_0 4_0 2_0 2_1 1_0 1_0 1_0 21/3
4_2 3_2 3_1 2_0 1_1 1_0 1_0 1_0 16/6
5_1 3_0 2_1 2_1 1_0 1_0 1_0 1_1 16/4

FIG. 22.

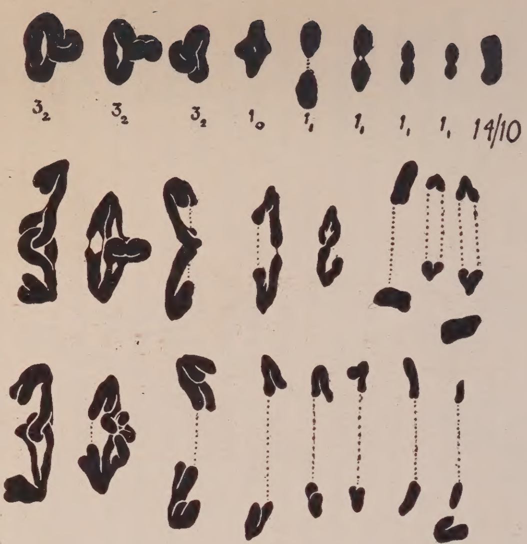

3_2 3_2 3_2 1_0 1_1 1_1 1_1 1_1 14/10

FIG. 23.

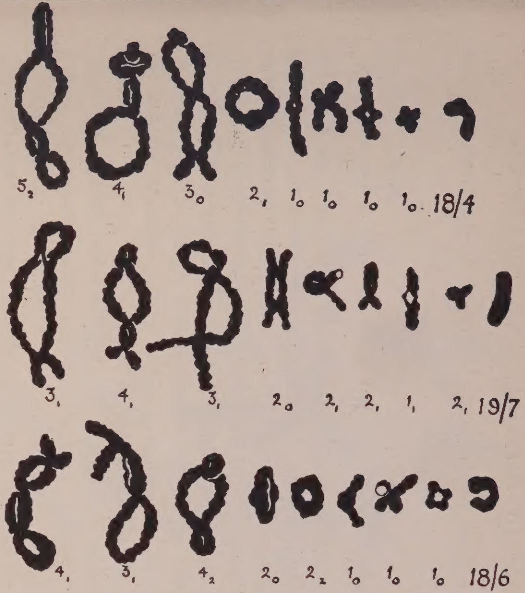

5_2 4_1 3_0 2_1 1_0 1_0 1_0 1_0 18/4
3_1 4_1 3_1 2_0 2_1 2_1 1_1 2_1 19/7
4_1 3_1 4_2 2_0 2_2 1_0 1_0 1_0 18/6

FIG. 24.

FIGS. 21–24.—The eight paired chromosomes of *Stenobothrus parallelus* and, rightmost, the unpaired sex chromosome, drawn separately. Three nuclei are illustrated at each stage to show the kind of natural variation that occurs in the form of the chromosomes, *i.e.*, in the number and position of the chiasmata. Under each bivalent are given the total number of chiasmata and the number that are terminal. Fig. 21.—Middle Diplotene. Fig. 22.—Late Diplotene. Fig. 23.—Diakinesis. Fig. 24.—Metaphase and Anaphase. Note the increase in the proportion of terminal chiasmata in the later stages and the expansion of the middle loop in the three leftmost bivalents which have median chiasmata. The two leftmost bivalents at anaphase correspond exactly with the metaphase figures above them. × 2400. (From D. and Dark, 1932.)

following relationship of chiasmata to length in the three types of chromosome :

Length .	5 μ	9 μ	21 μ
Chiasmata .	2·0	3·6	6·2

A direct proportion has also been clearly shown in *Vicia Faba* for two types (Maeda, 1930). In many species where there is a big discrepancy between the sizes of the chromosomes, the smaller ones have a higher proportional frequency (*e.g.*, *Stenobothrus parallelus*, D. and Dark, 1932). Thus in most organisms the distribution of chiasmata is not strictly at random with regard to one another. But it seems to be at random in regard to the different parts of the chromosome—whether proximal or distal.

In one organism, *Mecostethus grossus* (Janssens, 1924 ; McClung, 1927), it has, however, been shown that the chromosomes do not pair along their whole length but only at the ends near the spindle attachments, which are terminal. Naturally, chiasmata can only be developed in the paired regions, and the result is a characteristic *localised* association of the chromosomes. There is usually a single chiasma immediately next to the spindle attachment.

In other species of *Mecostethus* and in related genera (McClung, 1914, 1927) and in *Fritillaria Meleagris* and some half-dozen other species of this genus (Newton and D., 1930, and unpublished) a similar condition is found, but in a less exaggerated form. Several chiasmata are formed, but most of them are in the neighbourhood of the attachment constriction ; it is therefore possible to distinguish between the bivalents with median and those with terminal attachment constrictions by the position of their chiasmata. But chiasmata are also found occasionally in distal parts of the chromosomes. The chromosomes appear to be completely paired at pachytene (Newton and D.), but a comparative study shows that they are not so closely paired as in the related species *F. imperialis*, which has chiasmata formed regularly throughout its length. Small unpaired loops are constantly found at pachytene. It is therefore probable that localisation of chiasmata is due to their random formation in paired threads whose pairing is localised either completely as in *Mecostethus grossus*, or partially as in *Fritillaria*

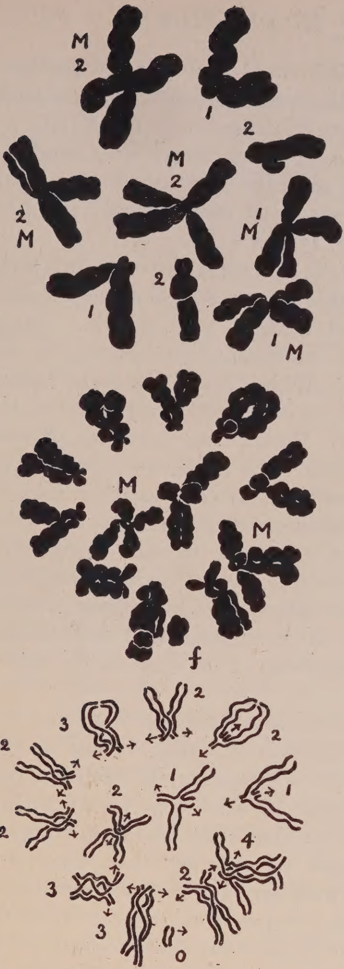


FIG. 25.—First metaphase in species of *Fritillaria*. Top, *F. ruthenica*, $n = 9$. Middle, *F. pontica*, $n = 12$, and one unpaired fragment (× 1500). Bottom, a line diagram representing the structure of the bivalents in the same, in terms of their chromatids. The numbers of chiasmata in each bivalent are given. The arrows show the positions of the spindle attachments. M, chromosomes with median attachment. Localisation is complete in *F. ruthenica*, incomplete in *F. pontica* (*cf.* Ch. III., 4 (i), and Fig. 15 and p. 80). × 1600 (D., unpublished).

Meleagris. The differential behaviour as to parts of the chromosome is analogous to differential behaviour as between different chromosomes in precocious condensation (*v*. Ch. XIII).

The occurrence of these forms with marked localisation of chiasmata warns us that slight variation in local distribution of the chiasmata may occur very generally and have so far passed unnoticed (*cf*. Fig. 25).

With regard to the chiasmata formed in each bivalent at diplotene it may be said that two is the commonest number, and a range between one and three is very general. Certain Liliaceæ and Leguminosæ are outstanding exceptions in having frequently higher numbers (*v*. Table 46), and the male Tettigidæ (Orthoptera) are exceptional in usually having only one (Fig. 82).

(iii) **Diakinesis.** During and following chiasma-formation the chromosomes contract still further in length and begin to assume a more rounded outline until *diakinesis*, the stage of greatest linear contraction. The chromosomes are then shorter and broader than at metaphase of a somatic mitosis, except where, as in some Lepidoptera, the mitotic contraction is already a maximum, and the chromosomes are spherical at metaphase even at mitosis. They occupy, whether in an organism with large or small chromosomes, less than one-hundredth of the space of the nucleus. The nucleoli disappear.

Where, as in *Pristiurus* (Rückert, 1892) and *Scolopendra* (Bouin, 1925), considerable size variations occur in the nucleus during prophase, the chromosomes vary in size proportionately, probably through their retaining the same water-content relative to the nuclear sap. (Bouin has unnecessarily interpreted his observations of these changes as meaning that there are two kinds of spermatocytes, with large and with small chromosomes.)

The relationship between the volume of the nucleus and of the chromosomes in different organisms is perhaps not so variable as would appear from a comparison of illustrations of this stage in organisms with chromosomes of different sizes, as the following estimate (necessarily a very rough approximation) indicates (Table 13).

The separate bivalents are evenly distributed in the diakinesis

TABLE 13

Size of Nucleus and Chromosomes at Diakinesis

	Prunus cerasus (D., 1928).	*Tulipa*, 3*x* (Newton and D., 1929 *b*).
Diameter of nucleus	8·3μ	24·4μ
Average length of chromosomes . .	0·5μ*	6·1μ
Diameter of chromatids . . .	—	0·4μ
Number of chromosomes . . .	32	36
Volume of nucleus	299 cu. μ	7600 cu. μ
Volume of chromosomes . . .	2·1 cu. μ	55·3 cu. μ
Ratio, nucleus/chromosomes . .	142	138

* Approximately spherical.

nucleus. Where they are few in number and much condensed this means that they lie chiefly on the periphery.

In some organisms the bivalents themselves continue to show no special internal changes. Successive loops between chiasmata lie at right angles to one another, but no general distinction can be made between them in regard to size (*e.g.*, *Vicia Faba*, *Fritillaria imperialis*). In others one loop is distinguished from the others by the sharp repulsion between its arms—so sharp that they are drawn out into fine threads as they are afterwards at late metaphase (Fig. 28). In these it is often found that the chiasmata are now no longer interstitial—they have been gradually pushed along to the ends of the chromosomes. All connection between the chromosomes may then seem to be broken by the strong repulsion, especially where the chromosomes are small, and this interpretation has been put upon such configurations (Keunecke, 1923). Comparative study shows that a different interpretation is possible. This will now be considered.

(iv) The Movement of Chiasmata. In *Fritillaria* the change from diplotene to diakinesis is unaccompanied by any marked change in the structure of the paired chromosomes. The chiasmata are almost stationary and are therefore to be found distributed at diakinesis as they arose—either localised or at random.

In other organisms a change takes place. This is seen in its extreme form in *Primula* (D., 1931 *a*) and *Campanula* (Gairdner and D., 1931). It has three obvious characteristics :—

(i) The total number of chiasmata is reduced in each bivalent.

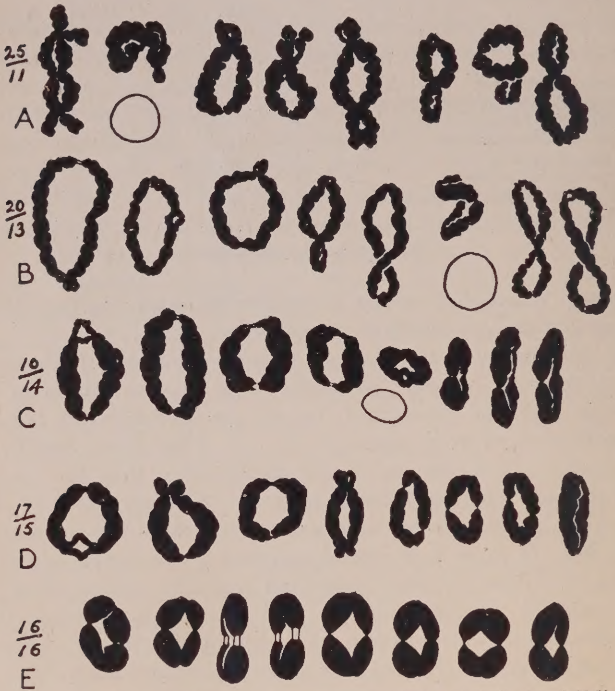


Fig. 26.—The eight paired chromosomes of *Campanula persicifolia* drawn separately, at successive stages between diplotene and metaphase to show the changes undergone with complete terminalisation. The numbers of chiasmata, total and terminal, in such nucleus are given at the side. D. is earlier than C. The nucleolus is shown in outline. × 3000. (From Gairdner and D., 1931).

(ii) The chiasmata come to be concentrated nearer the ends.

(iii) These changes taking place *pari passu* eventually leave all the bivalents associated terminally and the number of chiasmata reduced to the number of ends associated—if this end-to-end association be indeed a chiasma, a question which will be considered later in detail. At present it is enough to note that the connection is not between two whole chromosomes, but between their component chromatids. Each chromatid, which has been connected side-by-side with one partner, comes to be connected end-to-end with another, and hence the terminal association means a change of partner after the lateral association. It therefore has the essential morphological properties of a chiasma (Ch. XII).

A true terminal chiasma can be readily distinguished from a sub-terminal one both at diakinesis and at metaphase, when one or both of the limbs of each of the chromosomes connected by it are repelling one another, *i.e.*, when they include the attachment constriction. The connections between the chromatids are then reduced to the minimum and are drawn into fine threads by the tension they undergo. In the absence of this tension there is no sharp demarcation between the terminal chiasma and the interstitial chiasma that is nearly terminal.

There can be no doubt that this change of arrangement in the chromatids is essentially the same as that described in certain bivalents of *Phrynotettix* by Wenrich (1916). It was then said that the chiasma arose from the meeting of splits separating the four chromatids along two planes and that the movement was due to one split gaining at the expense of the other. It may equally be described as two types of association of chromatids replacing two others (a description that will be found most convenient for theoretical consideration) or as the movement of a chiasma along the chromosome towards the end or away from the attachment constriction. This last point of view has suggested the expression "terminalisation" (D., 1929 *c*).

However many chiasmata are terminalised, the chromosomes remain associated by terminal chiasmata. It must therefore be assumed that they merge at the ends, for if they fused interstitially they would sometimes cancel one another out. Why they do not do so when they fuse at the ends is a problem that will be specially considered later (Ch. XII).

(v) **Metaphase : the Structure of Bivalent Chromosomes.** After diakinesis the wall of the nucleus disappears and the spindle develops as in ordinary mitosis. The bivalent chromosomes arrange themselves on the equator with their attachment constrictions as usual in the axis of the spindle, but each chromosome, *i.e.*, pair of chromatids, now acts as though it had a single attachment, and the two attachments of the bivalent (whose repulsion has momentarily lapsed) now begin to repel one another actively, so that they are separated by the two segments joining them to the first chiasma. If these segments are short they are drawn out, as is the case with small chromosomes at diakinesis, into a fine thread.

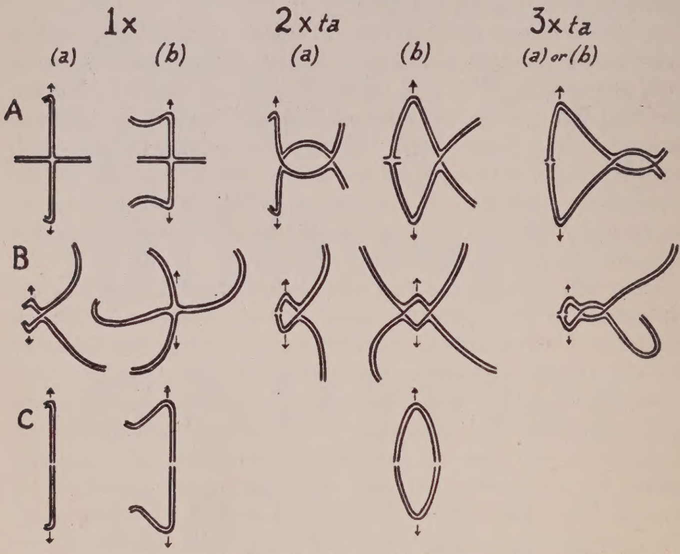


FIG. 27.—Diagram to show the chromatid structure of representative types of bivalents at metaphase. *A*, with unterminalised, random chiasmata. *B*, with unterminalised, localised chiasmata. *C*, with completely terminalised chiasmata. x, xta : chiasma and chiasmata. (*a*), with subterminal spindle attachment (represented by arrow) ; (*b*), with submedian attachment. (From D., 1931 *c*.)

The successive loops between chiasmata have, with the increasing thickness and, presumably, rigidity of the chromosomes, come to lie in planes at right angles to one another before diakinesis. This condition is still more strongly developed at metaphase, and is indeed the chief criterion of the existence of chiasmata at this stage.

Metaphase bivalents are therefore found to fall into various types according to (i) size of the chromosomes ; (ii) position of their attachment constrictions ; (iii) the number and position of the chiasmata, and especially the distance of the nearest chiasma from the attachment constrictions. Hence all metaphase bivalents fall into classes of which types are illustrated in the diagram (Fig. 27). The three classes as determined by the position of the chiasmata are as follows : *A*, those with random chiasmata ; *B*, those with chiasmata localised near the attachment constriction ; *C*, those with chiasmata confined to the ends or near the ends of the chromosomes, following terminalisation.

These classes are readily explained by reference to the observations of the origin of chiasmata at diplotene and their later movement in terminalisation. It is to be noticed especially that, at metaphase, bivalent forms are to be found which correspond with different stages of terminalisation, and it is evident from observations on *Rosa* (Erlanson, 1931 *c*) that this is due to the process being interrupted before completion by the onset of metaphase, after which it proceeds no further.

We have as the extreme type of terminalisation organisms in which interstitial chiasmata have never been observed at metaphase, *e.g.*, *Rhoeo discolor* (Fig. 42, D., 1929 *c* ; Koller, 1932 *c*).

Secondly, we have organisms in which a proportion of interstitial chiasmata are found, *e.g.*, *Circotettix*, *Matthiola incana* and *Rosa* (Fig. 45).

Finally we have organisms in which terminal chiasmata occur fairly frequently, but since there is no appreciable reduction in the number of chiasmata between diplotene and metaphase the occurrence of terminal chiasmata is presumably due to the terminalisation of only the distal chiasma, accompanied no doubt by slight movement of the proximal ones—*e.g.*, *Stenobothrus*, *Mecostethus*, *Fritillaria imperialis* and *F. Meleagris* (Figs. 21–24).

All chromosomes association at metaphase that is derived directly from pachytene association may therefore be regarded as derived merely by the formation and movement of chiasmata. Pairing

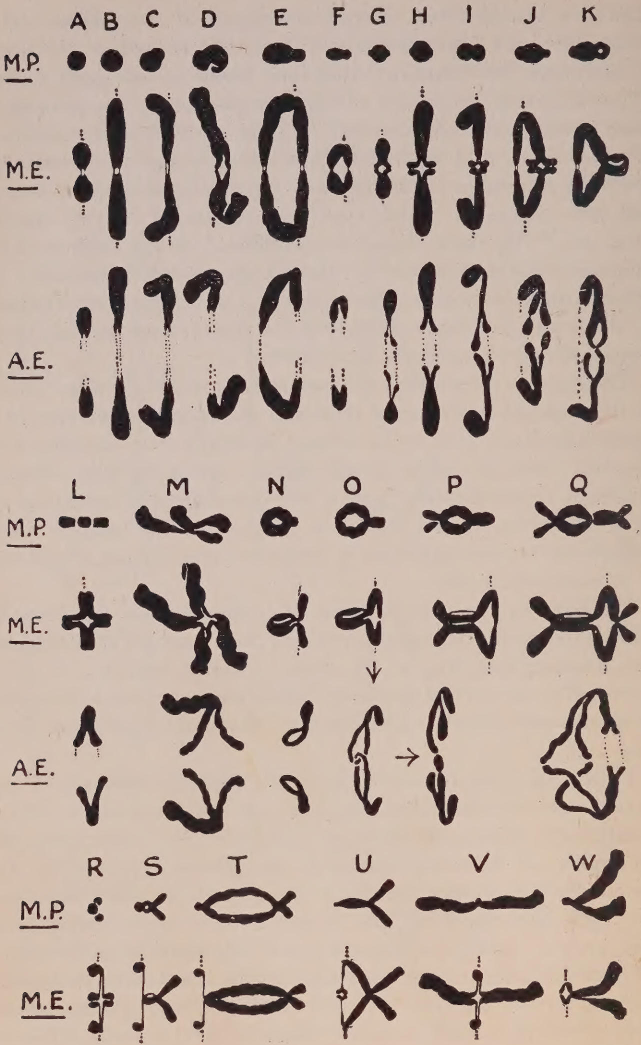

A
B
C
D
E
F
G
H
I
J
K
M.P.
M.E.
A.E.
L
M
N
O
P
Q
M.P.
M.E.
A.E.
R
S
T
U
V
W
M.P.
M.E.

FIG. 28.—Diagram showing forms of bivalents at the first division of meiosis. M.P., polar or top view of the metaphase plate. M.E., equatorial or side view of the same. A.E., equatorial view of anaphase showing daughter bivalents (not shown in types R to W, which correspond with earlier forms). Note that constrictions do not show at metaphase except by their position at the spindle attachment. Compare with line diagrams of structure (Fig. 27) as follows :

Type A,	1 chiasma (a) :—	G, H, L
	(b) :—	I, R
	2 chiasmata (a) :—	N (one terminal), S, T
	(b) :—	J, U
	3 chiasmata :—	K, O, P (one terminal), Q
Type B,	1 chiasma (a) :—	V
	(b) :—	M
	2 chiasmata (a) :—	W
	(b) :—	(Not shown)
	3 chiasmata	(Not shown, *cf.* Q)
Type C,	1 chiasma (a) :—	A, B
	(b) :—	C, D
	2 chiasmata (b) :—	E, F

Table

Classification of Organisms according to

1. Localised or semi-localised Chiasmata, Minimum Terminalisation.		2. Random Chiasmata, Minimum Terminalisation.	
Bombinator igneus ♀	Lebrun, 1902.	*Pristiurus*	Rückert, 1892.
Zoogonus minus	Grégoire, 1909.	*Tomopteris*	Schreiner, 1906.
Hippiscus	McClung, 1914.	*Humaria rutilans*	Fraser, 1908.
Tropidolophus	,, ,,	*Pamphagus marmoratus*	Granata, 1910.
Mecostethus spp.	,, 1927, 1928. Janssens, 1924.	*Dendroceolum lacteum*	Gelei, 1913.
Aggregata eberthi	Belar, 1926 *b*.	*Syrbula*	Robertson, 1916.
Barrouxia schneideri	Wedekind, 1927.	*Macropus*	Agar, 1923.
Mus norvegicus	Minouchi, 1929.	*Actinophrys sol*	Belar, 1922.
Fritillaria Meleagris	Newton and D., 1930.	*Stenobothrus* spp.	McClung, 1914. Wenrich, 1917. Janssens, 1924. Belar, 1929. D. and Dark, 1932.
Ranunculus acris	Sorokin, 1927.	*Hyacinthus orientalis*	Belling, 1925 *a*. D., 1929 *b*.
Chromacris miles, et al.	Saez, 1930.	*Uvularia*	Belling, 1925. ,, 1926.
Tettigonia albifrons	de Winiwarter, 1931.	*Amœba*	Belar, 1926.
Fritillaria ruthenica	D., unpub. (Fig. 25).	*Lilium* spp.	Belling, 1928 ,, 1931 *b*.
		Ephedra major	Geitler, 1929.
		Lathyrus odoratus	Maeda, 1930.
		Vicia Faba	,, ,,
		Fritillaria spp.	D., 1930 *c*.
		Taxus baccata	Dark, 1932.
		Eumeces latiscutatus	K. Nakamura, 1931.
		Kniphofia spp.	Moffett, 1932.

14

the Distribution of Chiasmata at Metaphase

3. Partly Terminalised Chiasmata.		4. Completely Terminalised Chiasmata.	
Leptynia atenuata	de Sinety, 1901.	*Myxine* and *Spinax*	Schreiner, 1904.
Brachystola	Sutton, 1902.	*Drosera*	Rosenberg, 1909.
Allolobophora	Foot and Strobell, 1905.	Lepidoptera	Federley, 1914. Seiler, 1926.
Salamandra	Schreiner, 1906.	*Forficula* spp.	Payne, 1914.
Circotettix	Carothers, 1913, 1917, 1921. Helwig, 1929.	*Acridium*	Robertson, 1915.
Phrynotettix magnus	Wenrich, 1916.	*Rhodites* and *Cynips*	Hogben, 1920.
Discoglossus pictus	Champy, 1923.	*Rana*	Witschi, 1924.
Matthiola incana	Lesley and Frost, 1927. Philp and Huskins, 1931.	*Melandrium album*	Meurman, 1925.
Zea Mays	Randolph, 1927. McClintock, 1929.	*Datura Stramonium*	Belling, 1927 *b*.
Humulus spp.	Kihara, 1929. Winge, 1929.	*Tropæolum majus*	Sugiura, 1927.
Crepis spp.	Babcock and Clausen, 1929.	*Belostoma*, etc.	Chickering, 1927.
Orgya antiqua	Cretschmar, 1928.	*Rumex Acetosella*	Kihara, 1927.
Nyctereutes	Minouchi, 1930.	*Nicotiana* spp.	Chipman and Goodspeed, 1927.
Prunus spp.	D., 1930 *a*.	*Orgya thyellina*	Cretschmar, 1928.
Cladophora spp.	Higgins, 1930. Schussnig, 1931.	*Bruchus*	Brauer, 1928.
Homo	Evans and Swezy, 1930.	*Œnothera* spp.	Catcheside, 1931 *b*. Gates and Goodwin, 1931. D., 1931 *d*.
Triticum spp.	D., 1931 *d*.	*Rhoeo discolor*	D. 1929 *c*.
Rosa spp.	Erlanson, 1931.	*Tradescantia virginiana*.	D., 1929 *c*.
Pisum sativum	Pellew and E. R. Sansome, 1931 ; E. R. Sansome, 1932.	*Aucuba japonica*	Meurman, 1929.
Nicandra	Janaki-Ammal, 1932.	*Campanula persicifolia*	Gairdner and D., 1931.
Anemone	Moffett, 1932.	*Primula sinensis*	D., 1931 *a* ; Dark, 1931.
Tulipa spp.	D. and Janaki-Ammal, 1932.	*Dahlia variabilis*	Lawrence, 1929.
Lathyrus tuberosus	Fisk, 1931.	*Anthoxanthum odoratum*.	Kattermann, 1931.
Festuca and *Lolium*	Peto, 1932.	*Alydus*	Reuter, 1930.
		Polemonium spp.	J. Clausen, 1931 *a*.

that is not derived from pachytene association will receive special consideration (Ch. XII).

The table classifying bivalent types is based on these considerations. The original distribution and later movement of the chiasmata is inferred where, as in so many organisms, it has not yet been observed, from the form of the metaphase chromosomes.

This kind of inference has been made in *Œnothera* (D., 1929, *a* and *c*) where at the time interstitial chiasmata had never been observed. Later work has shown such inferences to have been correct. They enable us to examine on a broader basis the conditions affecting terminalisation and localisation ; these conditions will be discussed later.

(vi) **Anaphase : the Separation of Chromatids.** When the bivalent chromosomes have been arranged on the metaphase plate so that their pairs of attachment constrictions lie in the axis of the spindle they divide ; the pairs of chromatids associated at the two attachment constrictions move to opposite poles. This means that in segments distal to a chiasma pairs of chromatids pull apart. And it is evident that they resist this separation, for bivalents which have the greatest length of chromatids to pull apart lag behind the rest (Plate IV, Plate VI, and Fig. 24). Such chromosomes are seen at anaphase with their two chromatids separated throughout their length. Conversely, the simplest and quickest separation is found amongst bivalents with terminal chiasmata. These merely break their terminal connections and pass to the poles without any separation of their paired chromatids. Indeed, they give no evidence, except at their tips, of their double structure. The extreme opposites are therefore found with localisation (Fig. 28, M, V, W) and with terminalisation (Fig. 28, A-E). For regularity in the separation of the paired chromosomes it is evident that uniformity in chiasma distribution is the essential condition, and the ideal is therefore complete terminalisation.

Terminalisation and likewise localisation of chiasmata are characteristic properties of species, and variation in the metaphase distribution of chiasmata must be regarded as another instance of the control exerted by specific factors or genes over the behaviour of the chromosome complement as a whole (*v.* Ch. III). Hence we can see in the very general occurrence of terminalisation an adaptation to the conditions of regular anaphase separation. The countervailing advantages of localisation will be considered in relation to the genetical theory (Ch. X and Ch. XIV).

In organisms having complete terminalisation, as a rule, an occasional bivalent has an interstitial chiasma, it is sharply distinguished at anaphase by its lagging. Such is the reason for the lagging of chromosomes described in the following species. (The list includes hybrids, which will be considered later ; in *Œnothera*, *Campanula* and *Aucuba* the cause of the appearance of the interstitial chiasma is probably arrest of terminalisation by change of homology in a structural hybrid, *q.v.*)

Phragmatobia fuliginosa	Seiler, 1914.
Physaloptera	Walton, 1924. (Large *X* chromosomes in homozygous sex.)
Stenobothrus spp.	Belar, 1929 *a* ; D. and Dark, 1932.
Aucuba japonica	Meurman, 1929.
Cycas revoluta	Nakamura, 1929.
Spinacia oleracea	Maeda and Kato, 1929.
Viola striata	J. Clausen, 1929.
Prunus hybrids	D., 1930 *a*.
Campanula persicifolia	Gairdner and D., 1931.
Œnothera biennis	D., 1931 *c*.
Dahlia (6*x* hybrid)	Lawrence, 1931 *a*.
Lachenalia glaucina	Moffett, unpublished.
Anthoxanthum odoratum	Kattermann, 1931.
Yucca flaccida	O'Mara, 1932.

The other side of the picture is shown by the *precocious* separation of bivalents in certain organisms. This is particularly noted where most of the bivalents have interstitial chiasmata. If then an exceptional one has a terminal chiasma, and especially if this is a short chromosome, it divides precociously (*e.g.*, *Mus musculus*, Painter, 1927 ; *Ranunculus acris*, Larter, 1932).

The observation of the structure of anaphase chromosomes is of great importance. It shows, first, that what might have been regarded at metaphase as "points of contact" between the chromosomes really were chiasmata. This is particularly significant in organisms (such as *Pisum* or *Œnothera*) where it has not been possible to trace the development of the chiasmata in prophase.

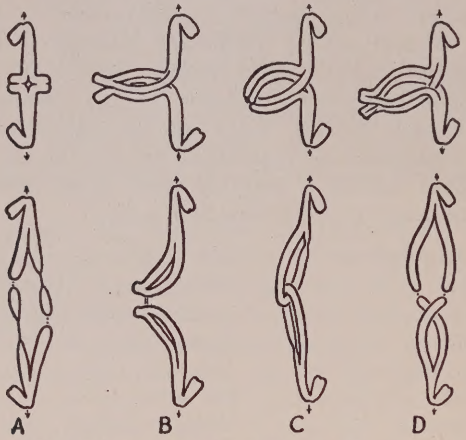


FIG. 29.—Diagram showing chromatid behaviour in anaphase separation of bivalents of different types. A. Single chiasma: one chromatid in each daughter chromosome shows a constriction. This constriction is momentary and has been best seen in living material (Belar, 1928, Fig. 266; *cf.* Janssens, 1924, Fig. 259; Belling, 1926 *b*, Fig. 6).

B and C. Two " compensating " chiasmata: the chromatids are associated distally to the second as they were proximally to the first (E. R. Sansome, 1931; *cf.* Janssens, 1924, Fig. 259; Belling, 1926 *b*, Fig. 6; Newton and D., 1930). The point at which the chromatids separate last appears to show a connection (D., 1929 *b*, Figs. 29 *a* and 56).

C. The loops formed by the two pairs of chromatids interlock (Janssens, 1924, Fig. 259). One loop then breaks its terminal association in separating (Belar, 1929 *a*, Fig. 9).

D. Two non-compensating chiasmata: the anaphase figures are asymmetrical in consequence (Janssens, 1924, Fig. 259; Newton and D., 1930).

N.B.—*Cf.* also Sakamura, 1915; Maeda, 1930, *a* and *b*.

It shows, secondly, the relationship of the exchange undergone at one chiasma to that undergone at the next (*i.e.*, of the observed exchange, apart from any genetical implications it may have). Two types of relationship are to be expected (Newton and D., 1930).

In one the second chiasma restores the association of chromatids that was lost at the first chiasma ; the two chiasmata may then be said to be compensating (again in a purely observational or " cytological " sense). In the other type the second chiasma does not restore the original association. The chiasmata are non-compensating. Both these types of relationship are found (Fig. 29) where anaphase chromosomes have been studied and are readily distinguished.

The two types of chiasma-combination correspond on the chiasma-type hypothesis (*q.v.*) to (i) single crossing-over in each of the four chromatids or recurrent double crossing-over in two chromatids ; and (ii) double crossing-over in one chromatid and single crossing-over in each of two others. In the first type the chromatids form a loop, rejoining one another distally ; the two loops may interlock, as observed by Belar in living material of *Stenobothrus*. Whether or not this has some significance in relation to the earlier occurrence of crossing-over is not yet known. In the second type the two chromatids are separated throughout their length, but on one side they lie apart, while on the other they cross their legs, as it were.

(vii) **Interphase.** The chromosomes pass to the pole in half the number characteristic of somatic mitoses. But since each consists of two chromatids instead of one, these are present in the normal number. We may say, therefore, the number of spindle attachments is reduced, the number of chromatids is unreduced.

When the chromosomes reach the pole they either reconstitute daughter-nuclei or they pass directly into a second division. In the first case the daughter-nuclei may pass into a fairly complete resting stage. It is then often found at the ensuing prophase of the second division which follows rapidly that the spiral structure of the chromosomes is still retained (Ch. II, 4 (i)). Further, in these circumstances the chromosomes regain, or partly regain, their normal mitotic length. Otherwise, as in many animals and dicotyledons, they remain contracted to the same degree as at the first division.

The loss of contraction is shown to be due to the occurrence of an interphase by an abnormality in *Gasteria* (Tuan, 1931). Under exceptional conditions, doubtless both genetic and environmental, shortening occurs in the length of the interphase with a corresponding lack of recovery to the length of a somatic mitosis found in the normal nuclei.

One constant distinction is observed at the prophase from the normal behaviour at mitosis: the two chromatids are held together only at their attachments. Elsewhere they actually seem to repel one another. This is perhaps to be associated with one of the unique properties of the interphase period between the two meiotic divisions, *viz.*, that there is no division of the chromosomes, that the associated chromatids are derived partly from association with other chromatids, or that the chromatids have been separated from one another for a long time. The theoretical significance of this will be considered later (Ch. XII).

(viii) **The Second Division.** The second division follows the course of an ordinary mitosis. The chromatids momentarily come together throughout their length. Where they are globular they lie in the axis of the spindle. They are pulled apart from their attachment constrictions. Four daughter-nuclei are formed, each with half the number of chromosomes of the mother-nucleus. Meiosis is complete.

4. MEIOSIS IN POLYPLOIDS

(i) **Prophase.** It is known from the fact that chromosomes may pair in parthenogenetic organisms (*q.v.*), that their origin, whether maternal or paternal, has no connection with pairing. Therefore in polyploids having several identical chromosomes of each type instead of two, we must expect pairing to occur indifferently amongst all the chromosomes of each type. But there are several different ways in which we might suppose this to come about. For example, at zygotene the threads might associate in pairs throughout their length, as they do in diploids. Or they might associate in threes or fours, according to the number present of each kind, to give a triple or quadruple thread at pachytene. Neither of these surmises holds good.

In both triploids (*Tulipa* and *Hyacinthus*), and tetraploids (*Hyacinthus*), the chromosomes come together in pairs. In a triploid, therefore, one thread is left out of association, while in a tetraploid two separate pairs are formed. But different pairs are formed at different points. Each particle of the chromosome is potentially independent of its neighbours, so that exchanges of partner take place here and there along the paired chromosomes, and the paired threads at pachytene in the tetraploid resemble

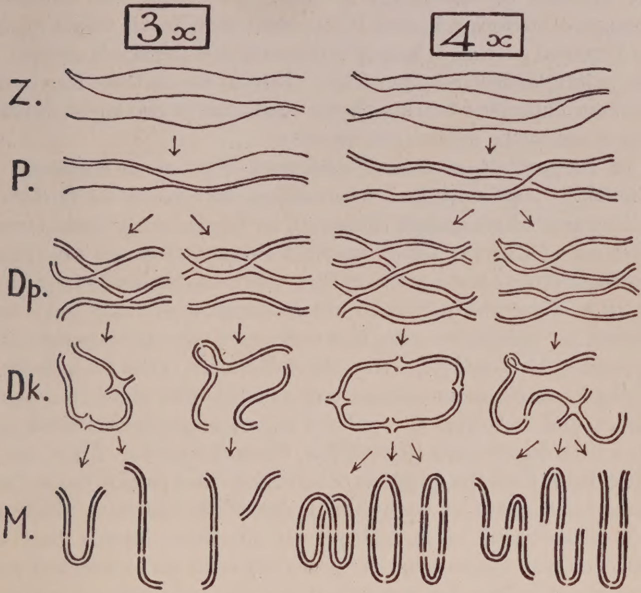


FIG. 30.—Diagram illustrating the structure of the pairing chromosomes during prophase and metaphase of the first division in triploids and tetraploids, with chromosomes having median spindle attachments and complete terminalisation. Z., zygotene ; P., pachytene ; Dp., diplotene ; Dk., diakinesis (with partial terminalisation) ; M., metaphase (with completed terminalisation). The lines represent chromosomes in the first two stages, chromatids afterwards. There are three stages of development when behaviour depends on chance : (i) choice of partner at zygotene ; (ii) formation of chiasmata at diplotene ; (iii) orientation in the spindle at metaphase. Variations through the last two chances are shown but the more complicated possibilities are omitted (*v*. Figs. 31–35, and Plate III).

those at diplotene in the diploid. As many as six exchanges have been observed in one association (Newton and D., 1929 ; D., 1929 *b*).

Three conclusions may be drawn from this behaviour : (i) The pairing properties of the chromosomes are specific to their constituent particles (chromomeres). (ii) The affinities of the chromosomes are satisfied by association in twos. (iii.) Since the number of changes of partner is limited it is evident that, as one would expect, an unpaired particle is largely influenced in its choice of partner by the pairing of adjoining particles. This, as we shall see later, must have an important bearing on the conditions of pairing in hybrids, which cannot be determined directly.

In the pachytene thread chiasmata arise as in diploids "at random." And since the chromosomes were paired at random it follows that where enough chiasmata are formed every possible combination of them is found amongst the chromosomes associated. Amongst other combinations is that where no chiasmata are formed at all between two particular chromosomes where they have been paired, for sometimes with free exchanges two chromosomes may happen to be paired for a very short distance. Thus there arise, in triploids, single chromosomes unassociated with their two homologues, and, in tetraploids, pairs of chromosomes unassociated with their homologous pairs (*Hyacinthus*, *Primula sinensis*). There can be little doubt from the prophase observations that pairing has in these cases taken place at pachytene between chromosomes which are left unassociated at metaphase. It therefore appears that the association of chromosomes is preserved after pachytene and until metaphase solely by the occurrence of exchanges of partner, chiasmata, amongst their constituent chromatids (D., 1929 *c*). This conclusion is borne out by quantitative observations of various kinds (*v*. Ch. XII). Its significance will be considered later.

Terminalisation occurs in the trivalents and quadrivalents that arise from chiasma-formation at diplotene as in the corresponding diploids. The associations produced in *Primula sinensis* (D., 1931 *a*; Dark, 1931) agree with the assumption that every pair of chromosomes that have been associated interstitially in one arm are at metaphase associated terminally in that arm. When chiasmata joining three or four chromosomes are terminalised to the same end a multiple chiasma is formed (see Figs. 32 and 35). This consists in the terminal association of the two chromatids of each of the chromosomes with chromatids of two different

PLATE III

PROPHASE OF MEIOSIS IN TRIPLOID *Tulipa*

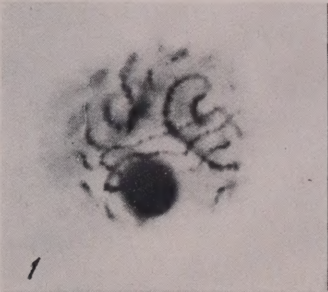
FIGS. 1 AND 2.—Zygotene, three chromosomes (running right and left in both nuclei) pairing, early and late stage. Note that the chromosomes are single threads and associate in pairs.

FIG. 3.—Beginning of diplotene, loops opening.

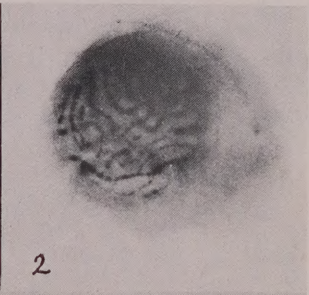
FIG. 4.—Late diplotene, exchanges of partner amongst chromosomes in trivalents and amongst chromatids at each chiasma.

FIGS. 5–7.—Diakinesis, three photographs of the same nucleus (*v.* Text-Fig. 31, second row).

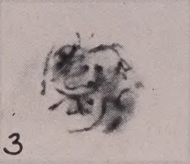
PLATE III



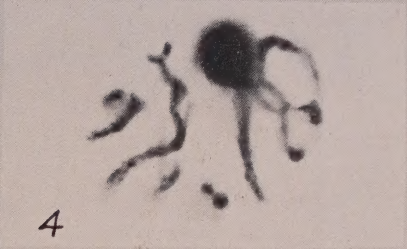
1



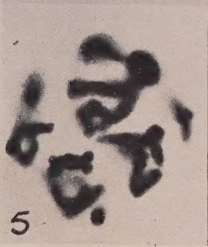
2



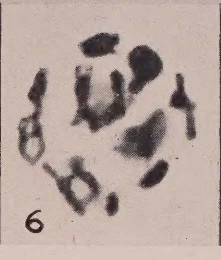
3



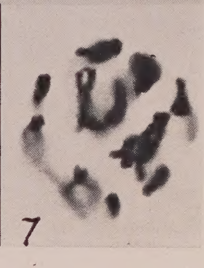
4



5



6



7

[*To face p.* 116.

chromosomes. Triple and quadruple chiasmata have been described in *Tradescantia*, *Aucuba*, *Primula*, *Œnothera* (Catcheside, 1931), *Rosa* (Erlanson, 1931), *Avena* (Kattermann, 1931), *Campanula* (Gairdner and D., 1931), and *Hemerocallis* (Dark, 1932). They also occur in *Datura* (Belling, 1927) and *Triticum* (Kihara, 1929 *et al.*).

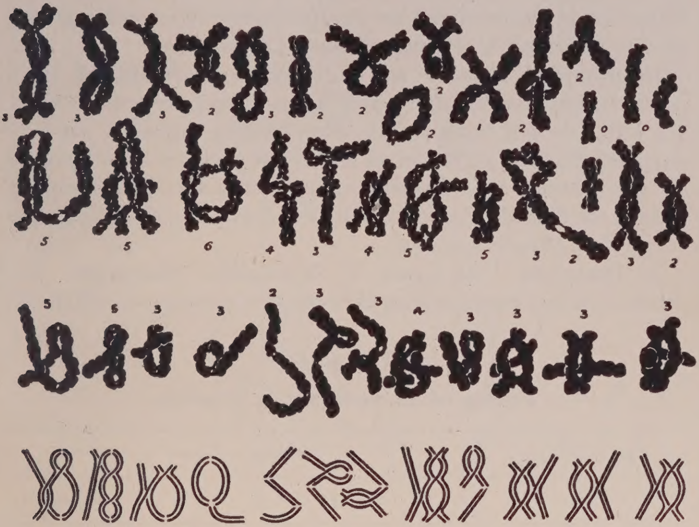


FIG. 31.—Chromosomes of complete nuclei of diploid and triploid *Tulipa* at diakinesis. The numbers of chiasmata are given under each configuration. Top, twelve bivalents in diploid *T. Gesneriana*. Middle, nine trivalents, three bivalents and above, three corresponding univalents in a triploid variety (*cf.* Plate IV). Bottom, twelve trivalents in the same variety, and a chromatid diagram of these. (Note the triple chiasma in the fourth from the left.) × 2000. (From D. and Mather, 1932.)

Thus each end of a chromosome in a triploid or in a tetraploid may be associated with all of the ends (two in the triploid and three in the tetraploid) that are homologous with it, *or* with some of them *or* with none at all. In other words, the kinds of terminal association at diakinesis correspond exactly with the kinds of interstitial association (by demonstrable chiasmata) observed earlier. Ten kinds of quadrivalents can be expected in this way, and they have all been found in *Datura* (Belling, 1927 *b*) or *Primula sinensis* (D., 1931 *a*). Clearly types where the chiasma is formed in each arm should be commoner, where the attachment constrictions are approximately median, than those where two are formed in one arm and none in the other. It follows, therefore, that the simple ring or chain quadrivalents are the commonest types, in forms with median attachments (*Primula, Datura, Campanula*).

In tetraploid *Primula* not only simple bivalents but very occasionally univalents (unpaired chromosomes) are found. Since the latter do not occur in the corresponding diploid it must be supposed that the exchanges of partner at pachytene are hindered by the presence of intervening chromosomes to a greater extent than in the diploid (*cf.* interlocking), and that pachytene association is therefore often incomplete.

(ii) **Metaphase : the Limits of Chromosome Association.** The extent to which corresponding chromosomes associate at metaphase has been described in a number of polyploids in which these chromosomes are supposed to be identical or nearly identical. In several triploids and tetraploids the chromosomes have been said to associate *fully*, *i.e.*, in *x* trivalents or quadrivalents (*e.g.*, *Canna*,

TABLE 15

Pairing of Chromosomes in Triploids

Triploids ($x = 12$).	Number of Univalents.											
	0	1	2	3	4	5	6	7	8	10	11	12
Lilium tigrinum .	4	12	14	**24**	9	4	2	—	—	—	—	—
Tulipa Gesneriana :												
Keizerskroon .	—	—	—	3	2	1	—	2	—	—	—	—
Pink Beauty .	1	1	3	3	—	—	—	—	—	—	—	—
Tetraploid ($x = 12$).												
Primula sinensis .	—	9	11	1	—	—	—	—	—	—	—	—

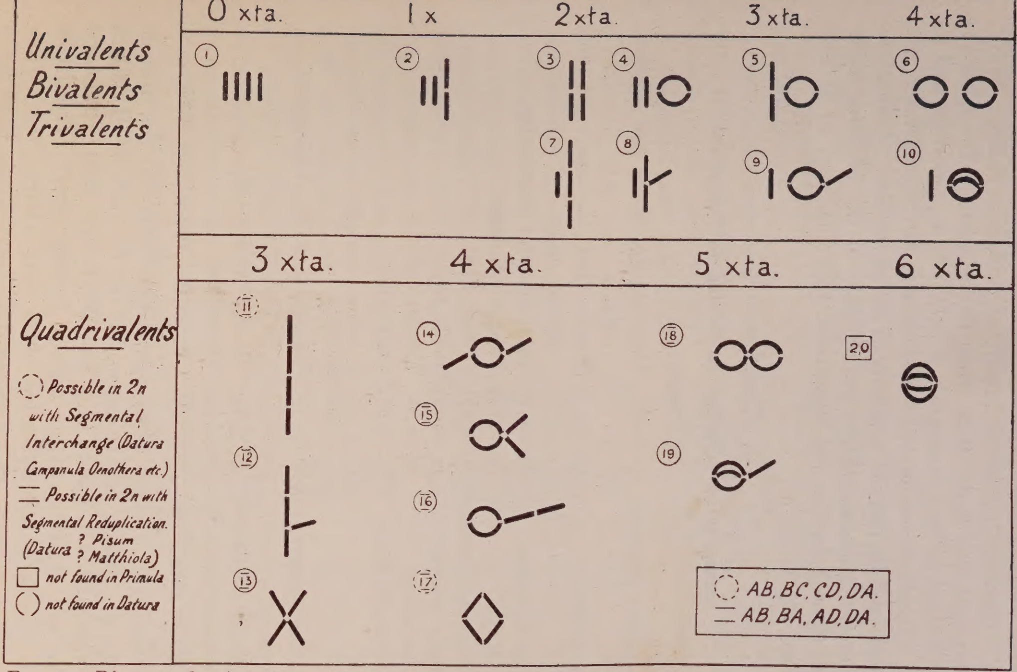

0 xta.
1 x
2 xta.
3 xta.
4 xta.
Univalents
Bivalents
Trivalents
①
②
③
④
⑤
⑥
⑦
⑧
⑨
⑩
3 xta.
4 xta.
5 xta.
6 xta.
Quadrivalents
11
12
13
14
15
16
17
18
19
20
( ) Possible in 2n with Segmental Interchange (Datura Campanula Oenothera etc.)
= Possible in 2n with Segmental Reduplication. (Datura ? Pisum ? Matthiola)
☐ not found in Primula
( ) not found in Datura
( ) AB, BC, CD, DA.
= AB, BA, AD, DA.

FIG. 32.—Diagram showing the multivalent and other configurations possible at diakinesis in a tetraploid with complete terminalisation. Certain of the associations of four are possible in diploid structural hybrids (*v.* Ch. V) xta = chiasmata; the numbers given are those necessary for the formation of the different types of association. (From D., 1931 *b.*)

Belling, 1921; *Datura*, Belling, 1927; *Primula Sieboldii*, Ono, 1927; *Hemerocallis*, Sinoto, 1929; *Hyacinthus*, Belling, 1928). Recent work has shown that, while full association does occur in most such forms in a proportion of nuclei, in a proportion also it fails. Trivalents are replaced by bivalents and univalents in the triploids and by pairs of bivalents in the tetraploids. Association is therefore both incomplete and variable, as the following table shows (from Takenaka and Nagamatsu, 1930; D., 1931 *a*; D. and Mather, 1932).

Table 16

Instances of Variation in Pairing in Polyploids

Triploids

Hyacinthus orientalis	$(x = 8)$	D., 1929 *b*; Stone and Mather, 1932.
Tulipa vars.	$(x = 12)$	Newton and D., 1929; D. and Mather, 1932.
Lilium tigrinum	$(x = 12)$	Takenaka and Nagamatsu, 1930.
Zea Mays	$(x = 10)$	McClintock, 1929.
Solanum Lycopersicum	$(x = 12)$	Lesley, 1929.
Primula sinensis	$(x = 12)$	Dark, 1931.
Allium nutans	$(x = 8)$	Levan, 1931.
Hemerocallis fulva	$(x = 11)$	Dark, 1932.

Tetraploids

Solanum Lycopersicum	$(x = 12)$	Jørgensen, 1928; Lesley and Lesley, 1930.
Hyacinthus orientalis	$(x = 8)$	D., 1929 *b* $(4x - 2)$.
Primula sinensis	$(x = 12)$	D., 1931 *a*.
Nicotiana suaveolens	$(x = 16)$	Goodspeed and Avery, 1929 *a*.

Where only a single extra chromosome is present in trisomic plants it behaves in the same way as do each of the extra chromosomes in a triploid (*e.g.*, *Solanum*, Lesley, 1929; *Matthiola*, Philp and Huskins, 1931; *Datura*, Belling, 1927). Tetraploids with complete terminalisation show very clearly the further interesting property that although the chromosomes must be in *symmetrical* associations at pachytene (every change of partner being reciprocal) their metaphase associations occur in all the possible ten types, of which only four are symmetrical (having both ends of all the chromosomes behaving similarly). Association is therefore variable, not only as affecting whole chromosomes but as affecting their parts.

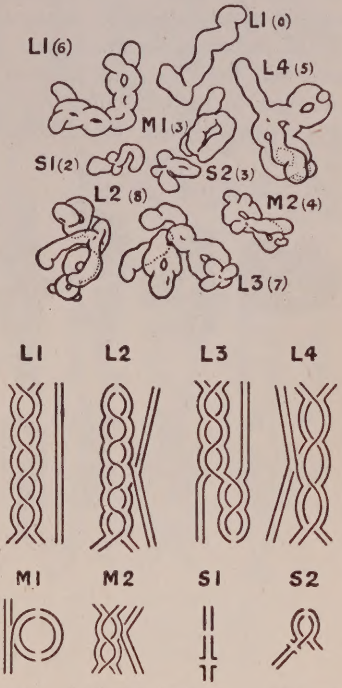


FIG. 33.—Seven trivalents and one long bivalent and univalent of a triploid (*Hyacinthus* $3x = 24$) in polar view at first metaphase and a chromatid diagram of the same. The numbers of chiasmata are in brackets. × 2000. (From Stone and Mather, 1932.)

Now it has been seen that the chromosomes of bivalents appear to be held together at diakinesis and metaphase merely by interchanges of partner between their chromatids, by chiasmata, for the chromosomes themselves repel one another. And it has been seen also that chiasmata are usually formed in a number proportionate to the length of the chromosome, or at least the length paired at pachytene, but varying in different nuclei both in number and position. The obvious conclusion is therefore that failure of chromosome association and its asymmetry is due to failure of chiasma formation owing to reduction in the length paired at pachytene, and hence that any two chromosomes are associated by virtue of a chiasma formed between them (D., 1929 *b*).

In order to test this hypothesis a closer analysis of chiasma formation in triploid *Tulipa* and *Hyacinthus* has been attempted

(D. and Mather, 1932; Stone and Mather, 1932). It is found that in *Tulipa* the proportion of univalents (with no chiasmata) as well as of chromosomes with different numbers of chiasmata can be approximately predicted on the assumptions:—(i) that the lengths of the chromosomes which pair at pachytene vary, as might be expected, from the randomness of association observed at this stage amongst the three chromosomes (only two of which can be paired at any one point), but the variation is very high, as though it were due to random association of a *small* number of "pairing blocks"; (ii) that the numbers of chiasmata formed in these paired lengths vary in the usual way; and (iii) that the association of the chromosomes at metaphase is conditioned by the formation of the chiasmata.

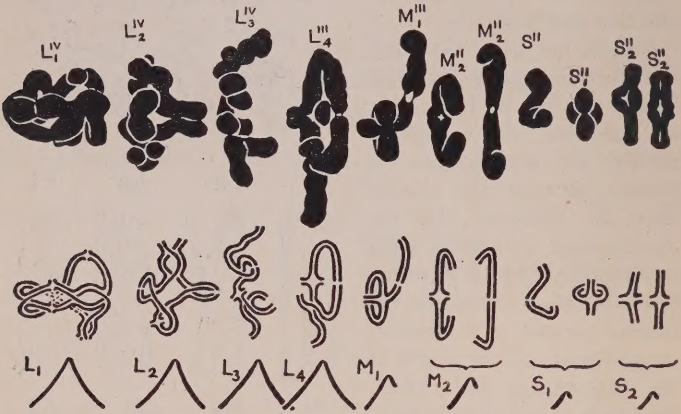


FIG. 34.—Side view of first metaphase in a $4x - 2$ *Hyacinthus*, with diagram of chromatids and mitotic chromosome types. (One medium and one long chromosome are lacking of the tetraploid complement.) × 2000. (After D., 1929 *b*.)

In triploid *Hyacinthus* there are three types of chromosomes, long, medium and short, with average frequencies of chiasmata amongst the three chromosomes of each kind of 6·2, 3·6 and 2·0 respectively (*i.e.*, in proportion to their length). As expected, the three types have distinct frequencies of univalents—2·8, 0·1 and 11·9 per cent.

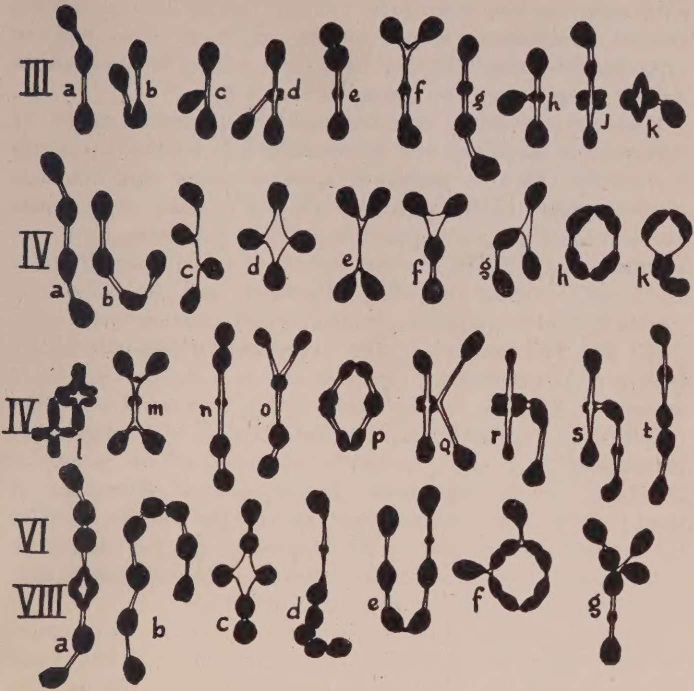


FIG. 35.—Multivalent configurations of small chromosomes, seen in side view of first metaphase. Roman numerals show the number of chromosomes in the configurations. III a–c, IV a–k, and VI b, c and f, have only terminal chiasmata. The rest have some interstitial chiasmata. IV c has an imperfect quadruple chiasma (*cf*. Ch. XII), IV d a perfect one. × *ca*. 6000.

These figures have been found in *Prunus* (D., 1928, 1930 *a*, Meurman, 1929), *Pyrus* (D. and Moffett, 1931; Moffett, 1932), *Solanum* (Jørgensen, 1928), *Primula* (D., 1931 *a*), *Galeopsis* (Müntzing, 1932), and will probably be found in many other genera where they have previously escaped notice.

respectively. The high frequency of univalents amongst the short chromosomes is explained by the low frequency of chiasmata. The fact that the long chromosomes have a slightly higher frequency than the medium ones is attributed to the interference with free assortment resulting from their extreme length, for they are the longest chromosomes known in any organism. This may be expressed by saying that they have fewer pairing blocks than the shorter chromosomes, two instead of four or five.

More direct evidence that chromosomes are held together by chiasmata at metaphase will be considered in relation to pairing in hybrids. For the present it must be noted that this view conflicts diametrically with the old theory that chromosomes are held together at metaphase by an affinity between them, and adequately explains the present observations, while the old theory leads one to expect uniformity, symmetry, and completeness in pairing instead of variation, asymmetry and incompleteness.

(iii) **The Two Divisions.** The arrangement of multiple bodies, with several attachment constrictions, in a bipolar spindle is inherently irregular. The result seems to depend on three conditions : (i) the arrangement of the chiasmata in the multivalent chromosome ; (ii) the spatial relationship of the points of attachment of the component chromosomes, as determined by their position in the chromosomes, and by the position in which the chromosomes are held by the chiasmata ; (iii) the relationship of the size of the chromosomes to the area of the equatorial plate, *i.e.*, whether the chromosomes are crowded or not.

The first condition determines the rigidity of the combination, for multivalents with interstitial chiasmata seem to be less pliable than those with only terminal chiasmata, and for two reasons : the distance separating the attachment constrictions of the associated chromosomes is shorter, and the cross-arms of an interstitial chiasma strengthen the connection while a terminal chiasma opposes the minimum resistance to any kind of torsion. The configuration with interstitial chiasmata is necessarily three-dimensional, that with only terminal chiasmata is two-dimensional (*v*. Ch. XII).

The second condition determines whether or not the multivalent is physically capable of lying in one axis, as does a bivalent. The third determines whether there is room for the chromosomes to lie transversely across the plate, as is necessary if each is to separate or " disjoin " (to use a common phrase) from the one with which it is associated.

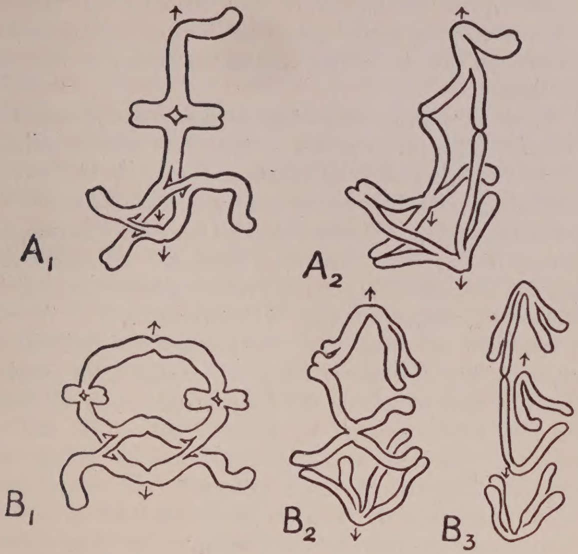


FIG. 36.—Diagram showing the division of trivalents in *Hyacinthus*. A_1 and B_1, metaphase ; A_2, B_2 and B_3 the anaphase forms to which they give rise. A divides into 2 + 1, B divides into $1\frac{1}{2} + 1\frac{1}{2}$. Arrows mark the attachment constrictions which are median. Note : (i) The chromatids are pulled apart distal to the chiasmata. (ii) Where, as in B_2, the chromatids of one chromosome are pulled in opposite directions, they are held together at the attachment constriction. (iii) The attachment constriction of a single chromatid is pulled back where it is associated with a chromatid of a whole chromosome. (After D., 1929 *b*. A_1, Fig. 28 f ; A_2, Fig. 29 b and 30 ; B_1, Fig. 28 r ; B_2, Fig. 29 n ; B_3, Fig. 31).

N.B.—Fig. B_2 shows that the holding together of the chromatids at the attachment is something essentially different from their attraction to one another in pairs elsewhere. This difference is probably described by saying that something at the attachment has not yet divided and the separation of the chromatids waits upon the division.

From the operation of these different factors the following differences may be observed :—

(i) The long axis of a multivalent may lie in the axis of the spindle or in the plane of the equator.

(ii) Each of the chromosomes may disjoin from those with which it is directly associated (provided it is not directly associated with more than two), or it may pass to the same pole with one or more of them.

(iii) Where an even number of chromosomes are associated they may divide evenly or unevenly; thus four chromosomes may divide into two and two or into three and one. In this way great differences may occur between the numbers of chromosomes in the two daughter-nuclei. *Prunus cerasus* (*4x*) gave exceptionally a distribution of 19 + 13 (Plate V). Similarly, tetraploid *Datura* (Belling and Blakeslee, 1924 *b*) and *Primula sinensis* (D., 1931) give germ-cells with unequal numbers of chromosomes.

(iv) Where an odd number of chromosomes are associated whole chromosomes may separate to the poles, or one of the component chromosomes may be left on the equator, and, after an interval, divide; the halves passing to opposite poles after the whole chromosomes. They then segregate at random in the second division. In triploids, therefore, germ-cells are formed with a random distribution of the chromosomes in the third set. This has been achieved by the random distribution, either of univalents (or odd members of trivalents) at the first division, or of daughter univalents (or odd members of trivalents) at the second division (*v.* Ch. IX). The detailed behaviour of unpaired chromosomes will be considered later (Ch. VI).

Where associated chromosomes pass to the same pole, all trace of their association is lost at the second division if an interphase occurs (*e.g.*, in *Hyacinthus*, *3x*; D., 1929 *b*); perhaps where chiasmata were interstitial and the interphase curtailed the association may be maintained occasionally (*e.g.*, *Pyrus Malus*, *3x*; D. and Moffett, 1930). The second division is therefore normal apart from such a difference as there may be between the numbers of chromosomes in the two daughter-nuclei.

5. CONCLUSION: THE PRINCIPLES OF CHROMOSOME PAIRING

The comparison of the behaviour of chromosomes during the prophase of meiosis in diploids and polyploids shows certain of the conditions of their pairing, as follows:—

(i) Zygotene pairing occurs only between similar chromosomes.

(ii) The unit of pairing is not the chromosome but the chromomere. Each chromomere is potentially independent of its neighbours at zygotene, as shown by changes of partner in the polyploids. Yet the number of changes of partner is limited, so that in effect the chromomeres act in *blocks* when they pair. Further, where exchanges occur, they probably lead to failure of pairing of the neighbouring segments on account of mechanical obstruction—whence the occurrence of unpaired chromosomes at metaphase in the tetraploid, although pairing is regular in the diploid.

(iii) Pairing at metaphase is conditioned by the formation of chiasmata in the pachytene thread. They are formed with an *average* frequency usually proportionate to the length paired at pachytene, but varying in different individuals, so that a short paired length may form no chiasma, and thus give no pairing at metaphase. Hence one chromosome of a set of three in a triploid may be unpaired at metaphase, although certainly pairing in a part of its length at pachytene. Hence also asymmetrical quadrivalents are very frequent in tetraploids, although the pachytene association must be always nearly symmetrical and complete.

(iv) Pairing at zygotene is only between pairs of chromosomes. Pairing between diplotene and metaphase is only between pairs of chromatids. Attraction, therefore, is at all stages between pairs of threads, whatever their value.

The first three of these conclusions are necessary for the analysis of chromosome behaviour in hybrids, which is our next consideration. The last is necessary for the analysis of the relation of meiosis to mitosis (Chs. XI and XII).

CHAPTER V

MEIOSIS IN STRUCTURAL HYBRIDS

Definition and Classification of Hybrids—Structural Hybrids—Fragments—Translocation and Interchange Heterozygotes—Unequal Chromosome Pairs.

> So wenig man eine scharfe Unterscheidungslinie zwischen Species und Varietäten zu ziehen vermag, ebenso wenig ist es bis jetzt gelungen einen gründlichen Unterschied zwischen den Hybriden der Species und Varietäten aufzustellen.
>
> MENDEL, 1866.

1. DEFINITION AND CLASSIFICATION OF HYBRIDS

THE systematist recognises a hybrid as an individual or type intermediate between two species, and he assumes it to be either a first cross or a derivative of a first cross. The geneticist's definition of a hybrid, which he owes to Mendel, is entirely different. On the one hand, he cannot draw a sharp line between species-differences and varietal differences, because he finds they are of the same kinds and differ only in degree (*cf.* Ch. XVI). Even in regard to inter-sterility, every gradation occurs between those pairs of species which are prevented from crossing in nature merely by incidental conditions and those which may be assumed to be intersterile under any conditions. For the geneticist, therefore, any cross between dissimilar races must be a hybrid, however slight their differences. On the other hand, the geneticist makes a sharp distinction between the first cross (F_1) and its derivatives, because the first cross is capable of showing segregation of the parental differences in its offspring, while its derivatives need no longer have these differences. An intermediate character is therefore for him no criterion of hybridity.

And finally the geneticist is not concerned with the difference between the parental zygotes but with that between the gametes which actually fused to make the hybrid. Thus it may happen that a cross between two dissimilar zygotes, if these were themselves hybrids, is constituted of two gametes that are identical; speaking in mendelian terms, *Aabb* and *aaBb* differ, but may give homozygous offspring *aabb*. Hence it may happen that a first cross between two taxonomic species in *Œnothera* is less hybrid than its parents, and the derivatives of such hybrids have been obtained which constitute pure lines in the strictest sense (Ch. XIV).

A hybrid (or heterozygote) must therefore be defined as *a zygote which* either *arises from the union of dissimilar gametes*, or *gives rise to dissimilar gametes* (regularly, *i.e.*, apart from mutation). For most purposes it will be found that these alternatives lead to the same result, and the second can be ignored except in relation to polyploids, in which hybridity requires special consideration. (Polyploids have chromosome sets corresponding with those of more than two ancestral gametes, and a simple definition of hybridity is therefore inapplicable to them.)

Hybrids have very generally the property of hybrid vigour or "heterosis" which is sometimes due to the accumulation of lethal or depressive factors in their parents and sometimes, perhaps, to an inherent virtue in the possession of a single dose of material in which the parents differ. Hybrids, both in plants and animals, are liable to abnormality, which is due to their having a new and untried hereditary complement. This liability is found in an exaggerated degree in one sex (the heterozygous sex) where the sexes are differentiated (Haldane, 1922) because the normal chromosome set of one species is not wholly represented in the hybrid and the deficiency may not be made up from the other. It may be said that the heterozygous sex in an animal hybrid is not strictly an F_1 hybrid at all, since it differs from the hybrid of the homozygous sex through the hybridity of one of its parents. Its properties are not therefore the characteristic properties of F_1 hybrids. They are incidental and depend on special genetic conditions.

The characteristic properties of hybrids depend, therefore, not on the properties of the parents, but on the differences between these properties which are seen, first, in the relation of the corresponding chromatin elements at meiosis and, secondly, in the differences between the offspring. The study of meiosis in non-hybrid forms and the variations already seen at mitosis enable one to classify hybrids and predict the kind of chromosome pairing that will be found in each class, as follows. (The term " hybrid " is reserved for the broader classes and the term " heterozygote " for the individual categories discussed later).

(i) NUMERICAL HYBRIDS. The zygote is derived from the union of gametes dissimilar in regard to the number of their chromosomes. Trisomic and triploid organisms which owe their origin simply to the reduplication of one or more chromosomes in one of the gametes are the simplest of this kind. It is irrelevant to the consideration of their properties at meiosis whether they result from mitotic or meiotic irregularities. The behaviour of these hybrids at meiosis has already been considered.

(ii) STRUCTURAL HYBRIDS. The zygote is derived from the union of gametes dissimilar in regard to the structure of their chromosomes, *i.e.*, the arrangement of their chromomeres or genes. The change in structure may also involve a change in number, as in fragmentation. From what we know of the pairing of chromosomes in polyploids we can predict that the chromosomes of these hybrids will pair according to the relationships of their parts, subject to these parts being long enough to allow of their occasionally pairing at pachytene and forming a chiasma in the length paired.

(iii) UNDEFINED HYBRIDS. The zygote is derived from the union of gametes dissimilar as a result of changes which cannot be defined. In this class may be considered those whose parental gametes either had the same number of chromosomes or a different number, through a change that cannot be identified. These hybrids may be supposed to be " undefined " simply because the structural differences between their chromosomes are too slight or too numerous to be readily detected. We may then expect three types of behaviour in this kind of hybrid at the first metaphase of meiosis, according to the frequency of differences between the chromosomes : (i) Normal behaviour owing to the differences being too slight to have a recognisable effect in reducing pachytene pairing and chiasma formation. (ii) A reduction in the frequency of chiasmata with or without occasional failure of pairing of the chromosomes. This failure will always show a curve of variation related to that of chiasma-formation. (iii) A reduction of chiasma-frequency to such a point that pairing fails entirely or almost entirely.

(iv) COMPLEX HYBRIDS. Another class of hybrids occurs in which the differences can be partly defined. Amongst these are the complex ring-forming and sex heterozygotes which form permanent self-reproducing types. Interchange, translocation and deficiency can often be inferred in them, but together with such changes others occur that can be located but not defined (*v.* Ch. XIV).

(v) POLYPLOID HYBRIDS (species or true-breeding varieties). The zygote is derived from the union of identical gametes, each of which is derived ultimately from the union of dissimilar gametes in an ancestor. These hybrids should be effectively true-breeding owing to the pairing and segregation of identical chromosomes derived from opposite immediate parents. In this case they would be functionally diploid. But they should also be liable to yield segregates owing to the occasional pairing of dissimilar chromosomes derived from their ultimate diploid parents (*v.* Ch. VII).

(vi) NUMERICAL-STRUCTURAL HYBRIDS. All types of cytologically observable hybridity may occur in the same organism, *e.g.*, in triploid *Œnothera* (Catcheside, 1931 *a*), *Triticum* (Kihara and Nishiyama, 1930), and *Avena* (Nishiyama, 1929), and in trisomic *Datura* (Belling, 1927 *b*). These will be considered in relation to structural hybrids.

(vii) MENDELIAN HYBRIDS (*sensu stricto*). Where a difference, which might be empirically described as a mendelian difference or group of differences, can be described directly in chromosome terms (as in the case of the trabant of *Matthiola* or the properties of ring-formation in various genera), it is no longer convenient to speak of it in mendelian terms any more than it is convenient to speak of "mutation" where the change can be defined as translocation or inversion. It therefore follows that mendelian differences for the cytologist are those which have no recognisable effect on chromosome behaviour. Probably most factor differences such as those found in *Drosophila* have a negligible effect on the pairing of the affected chromosomes. There is no evidence to the contrary, and in recent experiments in which wild type and mutant *Drosophila* have been compared genetically they show no difference in the frequency or distribution of crossing-over (Redfield, 1930) (*v.* Ch. IX). It will be seen, therefore, that cytological observations show many large differences, as in triploidy, which are incapable of mendelian analysis, while mendelian analysis shows many differences which are small in origin and incapable of cytological analysis. The visible spectra of variation shown by the two methods have different ranges which reveal two different aspects of the problem of variation.

2. MEIOSIS IN STRUCTURAL HYBRIDS

(i) **Method of Analysis.** The conclusion has been reached that only identical blocks or segments of chromomeres can pair at pachytene and form chiasmata which keep the chromosomes associated or " paired " at metaphase. On this assumption structural hybrids may be analysed. The differences between their chromosomes may be defined and hence the simple changes that have given rise to these differences specified.

Since terminalisation is usually complete in most of the organisms that have been studied from this point of view, the earlier association at pachytene, which is the characteristic of most importance, is only shown at metaphase by an association of the ends of the chromosomes. This association arises, however, in the ordinary way, as has been shown in particular cases (*v. infra*).

Where the end of one chromosome corresponds with the middle of another, the result of terminalisation is a lateral chiasma, and where this is fused with a normally terminalised chiasma a triple chiasma is formed (Fig. 39). There are two kinds of simple lateral chiasma: that derived from a single interstitial chiasma, and that derived from two compensating ones (Figs. 74 and 80). The significance of these will be discussed later (Chs. X and XII).

Where, in a diploid structural hybrid, several chromosomes are associated at meiosis it is better to speak of the configuration as a " group of three " or a " ring of four," reserving the terms trivalent, quadrivalent, and so on, for associations in which every segment is represented as many times as there are chromosomes concerned.

(ii) **Fragmentation and Fusion Heterozygotes.** The simplest kind

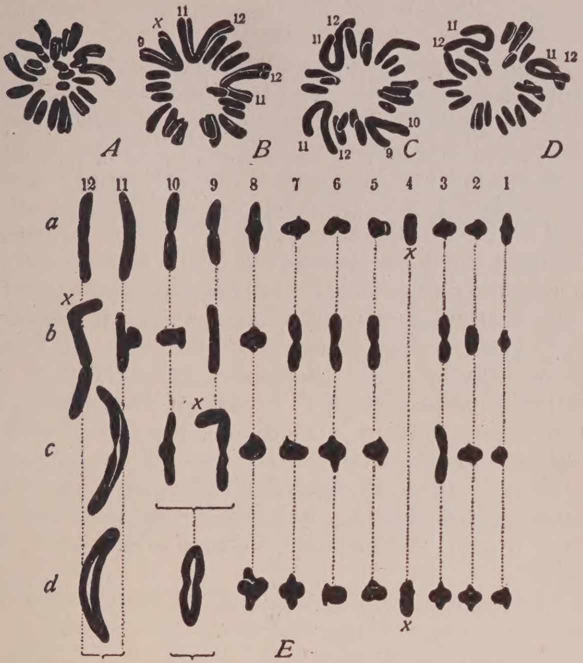


FIG. 37.—Permanent fusion of chromosomes shown by differences between *Hesperotettix brevipennis* (*A*) and different races of *H. viridis* (*B–E*). The complements shown are those of males and have a single unpaired sex chromosome (*X*, or No. 4, *v.* Ch. XIV). *A–D*, mitosis, polar view.

A, $2n = 23$; all chromosomes have terminal spindle attachments.

B and C, $2n = 20$; three pairs of non-homologous chromosomes have fused and have median attachments.

(In B, *X* and 9, 11 and 12, both pairs; in C, 9 and 10, 11 and 12, both pairs.)

D, $2n = 21$; two pairs have fused.

E. First metaphase of meiosis in side view; chromosomes drawn separately. *a*. The same type as A. *b*, $2n = 22$, *X* fused with 12. *c*. The same type as B. *d*, $2n = 19$. 9 fused with 10 and 11 with 12. All these are examples of fusion-homozygotes except in regard to the unpaired *X*-chromosome which necessarily gives heterozygotes in the male. (From McClung, 1917.)

of structural hybrid is that resulting from the union of gametes which differ merely in one of them having two chromosomes corresponding to two parts of one chromosome in the other, the difference arising presumably from fusion of the two in the first or fragmentation of the one in the second. Such an organism may be described as a " fragmentation heterozygote " and has been found in nature, and produced by crossing different races, in *Phragmatobia fuliginosa* (Seiler, 1925). The hybrid has regular pairing at metaphase of the two smaller chromosomes with ends of the large one. As a rule they pass to the opposite pole from it at the first division, but occasionally the smaller of the two fragments passes to the same pole with the large chromosome. The association is thus liable to the same kinds of abnormalities of distribution as are trivalents formed from three identical chromosomes (Plate VII).

The hybrid *Vicia sativa* × *V. amphicarpa* (Sveshnikova, 1929, *a* and *b*) behaves similarly ; two chromosomes of the first species are evidently derived by fragmentation from one that is represented in the second. They sometimes both pair at metaphase with the corresponding part of the larger homologue, and sometimes one of them fails to pair. It is apparently too short to establish a chiasma regularly.

The pairing in a cross between the domesticated silkworm (*Bombyx mori*, $n = 28$) and its wild relative (*B. mandarina*, $n = 27$) probably shows the same relationship, but one of the small chromosomes is sometimes paired laterally with the large one (Kawaguchi, 1928). This may be due to a " lateral chiasma " formed owing to terminalisation away from the spindle attachment of the large chromosome, if this is near one end.

Fusion heterozygotes have been found by McClung (1905, 1917) in *Hesperotettix* and *Mermiria*, and by Woolsey (1915) and Robertson (1916) in *Jamaicana subguttata*. In the former a chromosome which is found unpaired in the males (the sex chromosome) is fused with one of the other chromosomes. This other chromosome pairs normally with its mate, while the fused element, still attached, is as usual unpaired.

A hybrid between species of *Dicranura* (Lepidoptera) with 21 and 29 chromosomes is probably a fusion or fragmentation heterozygote, and consequently has pairing of groups of chromosomes (Federley, 1915).

The most general type of fragmentation heterozygote is that in which one (usually the smaller) product of fragmentation is present as a supernumerary or reduplicated chromosome, so that the organism is polysomic in respect of the segment concerned. This condition was first shown in *Metapodius, Diabrotica* and other Hemiptera (Wilson, 1905, *a* and *b*, 1909). In another hemipteran (*Alydus*, Reuter, 1930) supernumeraries occur, one of which is homologous with a part of a larger one, while both must be homologous with part of the sex chromosome, since all three may pair.

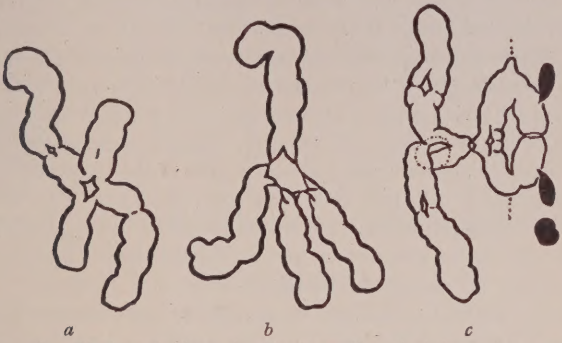


FIG. 38.—First metaphase in *Tradescantia virginiana* ($4x = 24$). *a*, an exceptional interstitial chiasma in a group of four chromosomes, due to arrest of terminalisation by change of homology. *b*, a normal quadrivalent held together by a quadruple chiasma. *c*, an association of six major chromosomes, and three homologous fragments (in black), two of them associated by lateral chiasmata at corresponding points in the major chromosomes. There is again an exceptional interstitial chiasma between two major chromosomes. (After D., 1929 *c*. *Cf.* Plate IV.) × 2400.

Recently large numbers of plants have been found with supernumerary fragments (*v.* Ch. III), and their pairing has been studied at meiosis in *Secale, Matthiola, Zea, Solanum, Tradescantia, Fritillaria* and *Datura*. It has the following characteristics.

(*a*) In an organism with negligible terminalisation in the major chromosomes, the fragments are always associated terminally (*e.g.*, *Fritillaria*, D., 1930 *c*). Thus three homologous fragments may form a triple chiasma before diakinesis. This indicates that slight movement of chiasmata occurs, and is noticed in the larger chromosomes which are nine times as long only by their distal chiasmata becoming terminal (*cf.* Ch. XII).

(*b*) The fragment is only associated at one end, in organisms with complete terminalisation, although the major chromosomes are associated at both ends (*e.g.*, *Tradescantia*, D., 1929 *c*; and *Datura*, Blakeslee, 1931). This is due to the fragment usually, on account of its shorter length, only forming one chiasma at prophase, or to its spindle attachment being subterminal, or to both causes.

(*c*) Where the fragment corresponds to an intercalary part of a major chromosome, it forms a lateral chiasma, after terminalisation, with the part of the major chromosome with which it is homologous (*Tradescantia*, *Fritillaria*, *Aucuba*, *cf.* Figs. 38, 39, and Plate IV).

(*d*) Fragments which are a small fraction of the length of the large chromosomes fail to pair in a proportion of cases. This failure is expected in organisms with a chiasma frequency proportional to the lengths of the chromosomes, on the assumption that pairing is determined by chiasma-formation, since the frequency of the chiasmata will be unchanged in the short new chromosomes, and they will therefore fail to form chiasmata and associate at metaphase, although doubtless associated earlier like the unpaired third chromosomes of triploids.

The frequency of their pairing will be predictable within limits, on this assumption, when three conditions are determined: (i) the chiasma frequency of the major chromosomes; (ii) the relative length of the fragments; and (iii) the " condition " of the fragments, *i.e.*, whether the fragments correspond to parts of the major chromosomes and whether they are in themselves disomic, trisomic, and so on.

The limits to exact prediction are set, first, by our not knowing the extent to which pachytene association is hindered by the difficulty of exceptionally small chromosomes finding one another during pairing at zygotene. If any hindrance occurs the effect will be to reduce the frequency of association. Secondly, limits to exactness are set by our not knowing the frequency with which two chiasmata will be formed in any given fragment. This occurrence will be favoured by low interference (*q.v.*) and will reduce the frequency of association.

TABLE 17.

Frequencies of the Pairing of Fragments in *Solanum Lycopersicum* (Lesley, J. W., and Lesley, M. M., 1929)

$2n = 24 + 2\,ff$. Fragments about one-quarter the average length of the major chromosomes. *C*, a major chromosome; *f*, a fragment, + indicates pairing.

Pairing.	$C+C+f+f$.	$C+C\,.\,f+f$.	$C+C+f\,.\,f$.	$C+C\,.\,f\,.\,f$.	Total.
No. of chiasmata of fragments * .	1·5	1·0	0·5	0·0	—
No. of observations .	13	39	5	8	65
Chiasmata formed .	19·5	39	2·5	0	61

* Where a fragment pairs with a major chromosome the fragment is said to have half a chiasma.

TABLE 18.

Chiasma Frequencies of Fragments (calculated from metaphase pairing on the chiasma theory of pairing, and compared with those of major chromosomes, D., 1930 *c*; Philp and Huskins, 1931).

Species.	Mean Chiasma-frequency of Major Chromosomes.		Proportionate Length of Fragment.	Number of Fragments (even or odd multiple).	Chiasma-frequency of Fragment.	
	All stages.	Metaphase.			Calculated.	Observed.
Fritillaria imperialis						
(i) "Yellow" .	2·58	—	1/9	6 ff.	0·29	0·22
(ii) "No. 10" .	4·96	—	1/9	3 ff (×2/3)	0·37	0·35
(iii) "Crown upon Crown"	4·33	—	1/9	3 ff (×2/3)	0·31	0·23
Matthiola incana						
(i) "Smooth" .	—	1·76*	3/4	1 f.	1·32	0·78
(ii) "Slender" .	—	1·58*	1/2	1 f.	0·75	0·36

* This frequency has been calculated from the behaviour of the trivalent. No correction for reduction of chiasma-frequency in trivalents need therefore be made for the fragments.

The observations lead to the following conclusions :—

(*a*) Fragments fail to pair, as predicted, and this failure is evidently due to failure of chiasmata, since clones of *Fritillaria imperialis* with low chiasma frequencies have a lower frequency of fragment-pairing than those with a high chiasma frequency.

(*b*) Pachytene association of fragments is probably liable to incompleteness, as expected, since the frequency is always below (and often considerably below) the expectation on the assumption of completeness.

(*c*) Pairing of large chromosomes with large and fragments with fragments is commoner than cross-pairing, which never occurs in *Solanum* (tetrasomic in respect of the fragment). In *Matthiola,* which is trisomic, the effect is still more drastic, since the odd fragment, deprived in competition of a partner amongst the large chromosomes, is evidently often left out of association and fails to reach two-thirds of the expected frequency. This indicates the importance of *competition* in pairing where there is a choice of partner : those which have the longest sequence of homologous particles will pair disproportionately often. This is particularly important in considering " differential affinity " in hybrid polyploids (Ch. VII) and *Œnothera* (Ch. XIV) and pairing in undefined hybrids.

(iii) Translocation Heterozygotes. When a portion of one chromosome has been translocated to another the heterozygote shows pairing of the corresponding segments. If one is terminal and the other interstitial, the result is a lateral chiasma. This has been observed in *Tradescantia virginiana, Aucuba japonica* and a *Viola* hybrid (J. Clausen, 1931 *c*). The special behaviour found in the hybrid *Vicia sativa* × *V. angustifolia dolichosoma* (Sveshnikova, 1929, *a* and *b*) can be taken as evidence of translocation. An open chain of four chromosomes is sometimes formed at meiosis, but more usually one or more, sometimes all, of these appear as univalents. Since the chromosome *E* of *V. sativa* is larger, and the chromosome *F* smaller than their homologues in the other species, the assumption of translocation is especially plausible ; the four chromosomes may be represented thus : *abc*, *defg* in one species, and *abcd*, *efg* in the other. It is to be noted that failure of pairing is particularly frequent in the shortest chromosome (*cf.* Fig. 43).

(iv) Reduplication Heterozygotes. In certain trisomic individuals of *Datura*, the so-called "secondary trisomics" (Belling and Blakeslee, 1924 *a*), the extra chromosome was found to have the same pairing properties at its two ends. It was therefore supposed that this chromosome consisted of two identical segments united at identical ends, *i.e.*, if the parent chromosome was *abcdef* then the new chromosome was *abccba*. It gave a series of configurations in accordance with this assumption (*v.* Fig. 44). The most interesting of these are the ones in which the two ends of the *same* chromosome are associated, by a terminal chiasma, for they show most clearly that the chromosome does not behave as a unit in pairing and that pairing is not determined by a difference in the origin of the mates. Similar configurations have been found in trisomic *Matthiola* (Philp and Huskins, 1931).

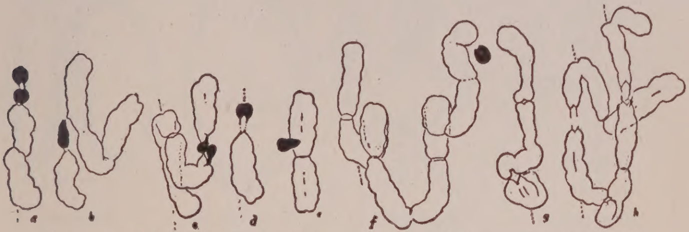
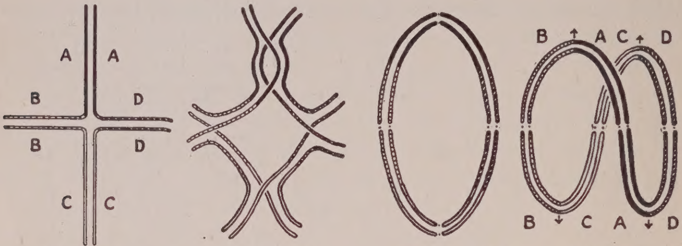


FIG. 39.—Pairing of major chromosomes and fragments (in black) in *Tradescantia virginiana*. *a*, two fragments and two major chromosomes. *b*, a fragment paired laterally at one end and terminally at the other end. *c*, a fragment paired by a triple chiasma with two major chromosomes. *d* and *e*, fragments paired by terminal and lateral chiasmata with major chromosomes. *f*, a fragment associated with a chain of eight major chromosomes. *g* and *h*, one major chromosome pairing with two parts of another, which are reduplicated, terminally and laterally by a triple chiasma. (From D., 1929 *c*.)

This condition has also been shown in regard to a small segment of the chromosome in tetraploid *Aucuba japonica* (Meurman, 1929 *b*) and *Tradescantia virginiana*. In all these forms triple chiasmata are formed presumably by terminalisation (D., 1929 *c*) just as though the homologous segments were all parts of different chromosomes. But the triple chiasma is lateral so far as one of its constituents is concerned.

(v) Interchange Heterozygotes. In many diploid plants, both natural races and artificial hybrids (*v.* Table 20) four, six or more chromosomes instead of forming two, three or more pairs at meiosis form a single association. This association, like those in polyploids, is not constant, but is liable to be replaced by smaller ones. Unlike those in polyploids, however, it is limited in its variation, as all associations must be in diploids, by the fact that each part of each chromosome has only one possible partner. Such variation as is observed is solely due to the failure of chiasma formation between some of the homologous pairs of segments.



Pachytene. *Diplotene.* *Diakinesis.* *Metaphase.*

FIG. 40.—Diagram showing the normal course of chromosome association in a simple interchange-heterozygote of the constitution *AB-BC-CD-DA* (type, *Campanula*). The A segments form two chiasmata at diplotene, the others one chiasma. Terminalisation is complete at diakinesis. The arrangement is "disjunctional" at metaphase; arrows denote the spindle attachments. (From D., 1931 *c*.)

The simplest condition which can lead to this behaviour is that of a heterozygote whose gametes contain chromosomes that have exchanged segments. Thus if such an exchange occurs in an organism of constitution *AB*, *AB*, *CD*, *CD* (each chromosome can be considered as made up of two segments when only a single structural change is involved) two new chromosome types will result: *BC* and *DA* (or *BD* and *AC*). The heterozygote derived from this interchange will have the constitution *AB*, *BC*, *CD*, *DA*, and pairing between all four pairs of homologous segments will give a ring of four when the chiasmata are terminal. Pairing between three of them will give a chain of four, and between two of them either two pairs or a chain of three and a univalent. In this way variations of chiasma formation will lead to variations in the size of the association, even though pairing is regular in the corresponding homozygotes, because the unit of pairing in this heterozygote is no longer a whole chromosome but a segment equal to about half a chromosome. The occurrence of an interchange of segments between non-homologous chromosomes was first inferred in trisomic forms of *Datura*, which will be considered later. In a number of diploids with rings or chains of chromosomes the whole course of meiosis and the special genetic properties of the heterozygote produced have now been determined. They may be summarised as follows :—

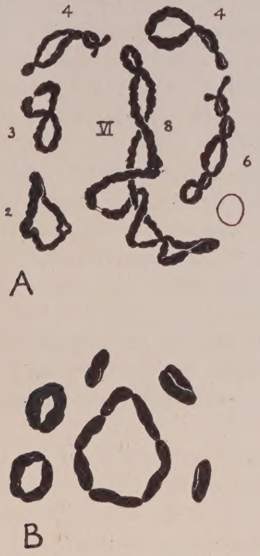


FIG. 41.—The development of a ring-of-six in a double interchange-heterozygote in *Campanula* (of the constitution, *AB-BC-CD-DE-EF-FA*). A, diplotene (with numbers of chiasmata given). B, diakinesis, (6) + 5 (2) = 16. (From Gairdner and D., 1931.) × 2500.

(i) Corresponding parts of the chromosomes can be seen to associate in pairs at pachytene, where all of them can be distinguished morphologically. There is an exchange of partner, where the homology changes, like that at pachytene in a tetraploid but obligatory (McClintock, 1931, *Zea Mays*).

(ii) Chiasmata are formed at random in the paired segments at diplotene (Gairdner and D., 1931, *Campanula persicifolia*).

(iii) These may remain nearly stationary (Pellew and Sansome, 1931, *Pisum sativum*), or they may be terminalised (*Campanula*, *cf. Œnothera*, Ch. XIV), in which case a simple ring or chain of chromosomes joined end to end appears at diakinesis (as found in *Datura*, *Œnothera*, etc.)

In *Campanula*, *Rhœo* and *Œnothera* unpaired chromosomes are frequently found owing to failure of association of both their ends. In *Campanula* even a ring of four may be replaced by a pair and two univalents, while in *Rhœo* and *Œnothera* a ring of twelve may break up in any of the conceivable ways—into 11 + 1, 10 + 2, 9 + 3, etc., or 9 + 2 + 1, 7 + 3 + 2, etc. This reduction of association is partly due in all probability to the pachytene association having been incomplete owing to the mechanical difficulty of making frequent exchanges of partner, as in the tetraploid *Primula sinensis*.

(iv) The configuration arranges itself on the metaphase plate just as a corresponding configuration would in a polyploid. This means that the behaviour of the chromosomes at meiosis is directly determined by mechanical conditions and is uninfluenced by genetical conditions. Thus an association of four in *Pisum* is arranged " non-disjunctionally " in about half the divisions, *i.e.*, so that chromosomes with associated segments will pass to the same pole (Håkansson, 1931 *a*). This is just like a similar association of four with interstitial chiasmata in a tetraploid *Hyacinthus*.

A ring of four in *Campanula*, on the other hand, arranges itself " disjunctionally " in about two-thirds of the divisions, *i.e.*, so that pairs of chromosomes with associated segments pass to opposite poles (Fig. 43). The same holds good for a quadrivalent in tetraploid *Primula sinensis*. The reason for this difference of behaviour is fairly evident. An association with interstitial chiasmata is

PLATE IV

MEIOSIS IN STRUCTURAL HYBRIDS

FIGS. 1 AND 2.—First metaphase in *Campanula persicifolia* ($2n = 16$). Fig. 1. Ring of four and six pairs. Fig. 2. Ring of six and five pairs. (Reproduced by kind permission of Miss A. E. Gairdner.)

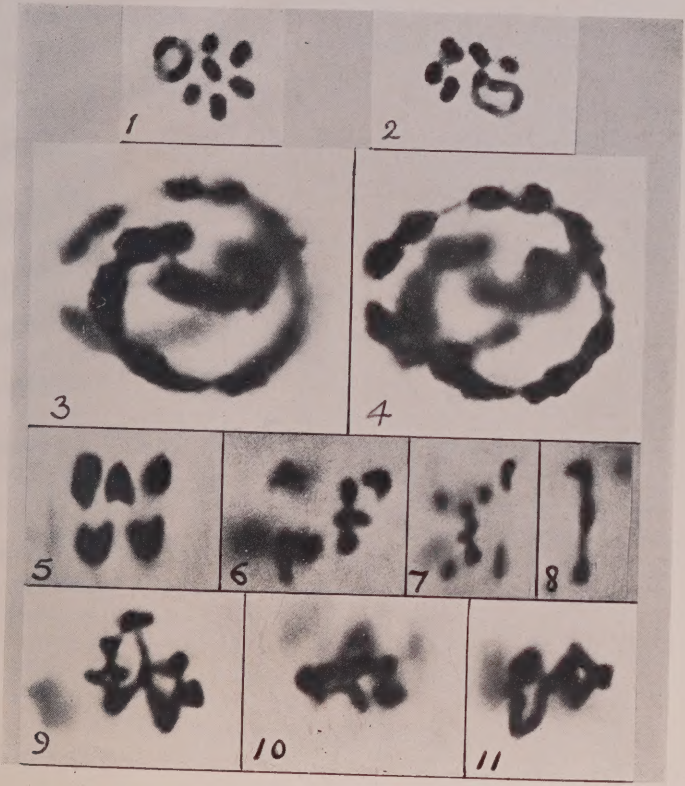
FIGS. 3 AND 4.—Diakinesis in *Rhœo discolor*, ring of twelve chromosomes, at two focuses. (Reproduced by kind permission of Dr. Pio Koller.)

FIG. 5.—Normally segregating ring of chromosomes at beginning of first anaphase in *Œnothera muricata*, five chromosomes shown.

FIGS. 6–8.—The exceptional occurrence of interstitial chiasmata in *Œnothera biennis* at metaphase and anaphase.
Fig. 7. The critical "figure-of-eight" configuration. Fig. 8. The interstitial chiasma leads to lagging at anaphase (*v.* Chap. X). (From D., 1931 *d.*)

FIGS. 9-11.—The same in *Pisum sativum* with a ring of six. Note the critical chiasma in Fig. 10. (*Cf.* Text-Figure. From E. R. Sansome, 1932.)

PLATE IV


1
2
3
4
5
6
7
8
9
10
11

[*To face p.* 142.

relatively rigid ; its shape shows little variation, and is determined by the number and distribution of the chiasmata. It is a three-dimensional system. An association with terminal chiasmata is extremely pliable ; the variation found in its shape shows that (as might be expected) any two chromosomes move freely in relation to one another unless they are associated at *both* ends. It is a two-dimensional system. Forces of repulsion associated with spindle formation are therefore able to effect regular disjunction of a ring with terminal chiasmata although they are powerless to distort a configuration held together by numerous interstitial chiasmata.

It appears that the proportion of non-disjunction is usually about 30 per cent. in rings of 12 or 14 chromosomes, just as it is in a ring of four or six (*cf.* Gairdner and D., 1931). This suggests that orientation of successive chromosomes in the ring usually begins at one part of the ring, and if begun disjunctionally will proceed regularly along the ring (*v.* Ch. XII).

(v) The genetical effects of non-disjunction are important. A ring of four segregates disjunctionally to give gametes *AB*, *CD* and *BC*, *DA*, non-disjunctionally to give *AB*, *BC* and *CD*, *DA*. Although in *Zea* and *Pisum* all the disjunctional products of segregation in the ring are viable, interchange heterozygotes are nevertheless semi-sterile. This is due to the non-viability of the 50 per cent. of non-disjunctional gametes, which lack one of the segments present in the parental complement. In *Campanula*, where there is less non-disjunction, partial sterility of the heterozygote is due to a second cause as well, *viz.*, the non-viability or lower viability of homozygous segregates. This is the probable explanation of the occurrence of the ring-forming heterozygote in nature, in *Campanula* as well as in *Œnothera* : the heterozygote breeds true because the homozygotes are not viable.

(vi) In all interchange heterozygotes so far found in plants the point of interchange is in the neighbourhood of the spindle attachment which is approximately median. In *Trimerotropis citrina* (Carothers, 1931) a ring of four has been found at first metaphase, which is evidently due to the individual being an interchange heterozygote (although the author does not recognise a causal distinction between meiotic pairing and permanent fusion). But here the spindle attachments are terminal, and when the ring-of-four is formed each chromosome has chiasmata with two other chromosomes on the *same* side of the spindle attachment. The ring therefore lies in the equatorial plane and is never disjunctional. The significance of this will be considered later (Ch. X).

(vii) The fact that interchange heterozygotes, having four, six or more chromosomes in a ring at meiosis, occur in nature gives a great interest to the origin and inheritance of the condition. They are on our hypothesis hybrids, produced by the union of dissimilar gametes. This dissimilarity is due to interchange taking place in an ancestor. There is no direct evidence to show whether the interchange gave rise to the heterozygote at once in nature or whether it gave rise to a new homozygous race which afterwards by crossing gave rise to the hybrid. The second is obviously the source of those ring-forms that have appeared in experiments. There is some reason to suppose, on the other hand, that where they occur in nature their preservation is due to the elimination of the homozygous products of the original interchange hybrid (*v. Œnothera*), *i.e.*, that they arose directly from the change without crossing between different parental zygotes.

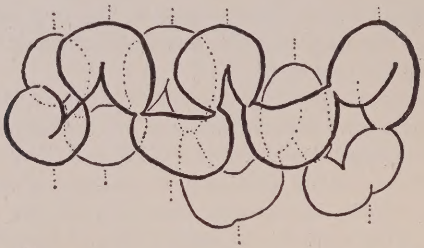


FIG. 42.—A ring-of-twelve arranged disjunctionally at first metaphase in *Rhœo discolor*. (From D., 1929 *c*.) × 2800.

In experiments with *Datura, Pisum* and *Œnothera*, hybrids with a ring of four have been obtained by crossing different homozygous races. The parents evidently differed in respect of one interchange, and the offspring (of the type *AB-BC-CD-DA*) may therefore be described as " single-interchange " heterozygotes. Hybrids with a ring of six or two rings of four are similarly "double-interchange" heterozygotes, and they have been produced either by crossing two parents which differed in two interchanges (*AB*, *CD*, *EF* and *BC*, *DE*, *FA*) as in *Datura*, or by crossing two single-interchange heterozygotes, which have one gametic type in common (as in *Pisum*, *Zea* and *Campanula*). From such a cross four kinds of progeny will result. Thus (*AB-BC-CD-DA*, *EF-EF*) × (*AB-AB*, *CD-DE-EF-FA*) will give homozygotes with simple pairing (*i.e.*, *AB-AB*, *CD-CD*, *EF-EF*), two kinds of "single" heterozygote (*i.e.*, the parental types) and one kind of "double" heterozygote with a ring of six (*i.e.* *AB-BC-CD-DE-EF-FA*). The proportions of the cytologically recognisable types will be 1 : 2 : 1, and the

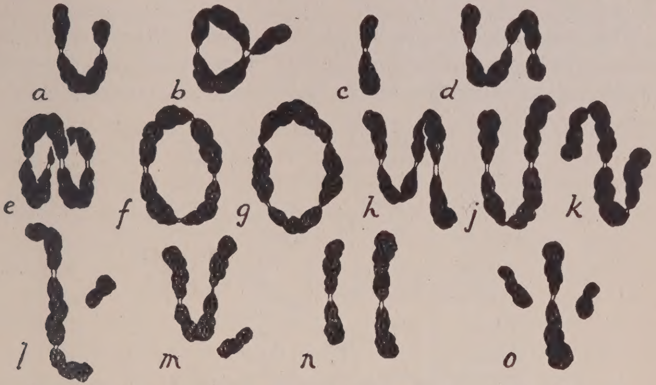


FIG. 43.—Configurations observed at first metaphase in diploid structural hybrids of the simpler kinds with complete terminalisation. *a*, fragmentation or fusion heterozygote (*e.g.*, *Vicia sativa* × *amphicarpa* or *Hesperotettix*). *b*, fragmentation-plus-reduplication heterozygote (*e.g.*, *Matthiola*); note triple chiasma. *c*, deficiency or reduplication heterozygote (*e.g.*, *Circotettix*). *d*, translocation heterozygote (*e.g.*, *Tradescantia bracteata* or *Vicia sativa* × *angustifolia*). *e—o*, simple interchange heterozygote (*e.g.*, *Datura*, *Campanula*) showing complete association in a ring-of-four and incomplete association in one or more chains. The chromosomes are represented as of three sizes—one long, two intermediate and one short in a constant order in the ring. *e* and *h* are disjunctional arrangements; *f*, *g*, *j*, *k* and *l* are non-disjunctional, the rest are doubtful. An interchange-plus-translocation heterozygote is illustrated in Figs. 71 and 72A. (*Cf*. Plate IV.)

inheritance can be described in mendelian terms, if each interchange is regarded as making an allelomorphic difference. Thus the cross is analogous to $AaBB \times AABb = 1\ AABB : 1\ AaBB : 1\ AABb : 1\ AaBb$ where $AaBB$ and $AABb$ are indistinguishable unless the chromosomes taking part in the rings can be distinguished (Fig. 41, Plate IV).

Where the interchanges in the two parents do not affect any chromosomes in common, the " double " heterozygote has two rings of four instead of one ring of six. Both these expected results have been found in *Campanula*, but in some crosses the homozygous forms, with simple pairing, are eliminated as mentioned above.

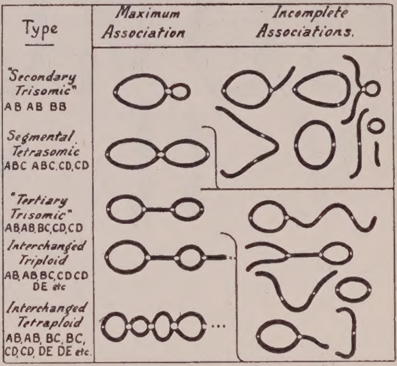

Type
Maximum Association
Incomplete Associations.
"Secondary Trisomic"
AB AB BB
Segmental Tetrasomic
ABC ABC.CD.CD
"Tertiary Trisomic"
AB.AB.BC.CD.CD
Interchanged Triploid
AB.AB.BC.CD.CD DE etc
Interchanged Tetraploid
AB.AB, BC, BC, CD.CD, DE DE etc.

FIG. 44.—Diagram to show the first metaphase associations possible in different polysomic and polyploid interchange heterozygotes with complete terminalisation. The incomplete as well as the complete associations are given for the secondary and tertiary trisomics (*cf.* Belling, 1927 ; Catcheside, 1931).

(vi) Polyploid Interchange Heterozygotes. A relatively interchanged condition was first found in the odd chromosome of a trisomic *Datura* (Belling and Blakeslee, 1924). This chromosome was apparently the result of interchange between two normal chromosomes *AB*, *CD*, so that the segmental constitution of the plant was *AB*, *AB*, *BC*, *CD*, *CD*. Plants of this type are known as " tertiary trisomics." They have various configurations, including a chain of five chromosomes (see Fig. 44).

In connection with these forms it is convenient to mention certain reduplication homozygotes, *i.e.*, organisms that are tetrasomic in respect of one segment, having four chromosomes that may be represented *abcd*, *abcd*, *efgd*, *efgd*. Since all four chromosomes can associate in the *d* segment, groups of four can be formed and, with terminalisation, a quadruple chiasma. Such configurations are found in *Datura* hybrids (Blakeslee, 1928) and probably in *Rosa* (Erlanson, 1931 *b*), *Matthiola* (Philp and Huskins, 1931), and *Tradescantia bracteata* (D., 1929 *c*). Probably configurations suggesting the same conclusions in *Œnothera biennis* (Cleland, 1923) are to be attributed to interlocking (*q.v.*).

Polyploid and polysomic interchange heterozygotes combine the large configuration made possible by their hybridity in structure with the variability in forming possible configurations which is characteristic of polyploids. Only the observation of " maximum association " (which is never found in complicated cases) or a knowledge of the ancestry can give the key to the constitution. The determination of their structure, therefore, requires extensive observation, and has only been conclusively carried out in a few forms.

A number of triploids have more than the haploid number of paired chromosomes at meiosis, although they are derived from diploids showing no evidence of a polyploid origin (*cf.* Ch. VIII), *e.g.*, in *Festuca*, *Fragaria* and *Triticum* with basic numbers of seven.

This can be accounted for in one of two ways : the diploid from which they have been derived may have been either (i) an interchange heterozygote or (ii) a reduplication homozygote. The triploid would have a segmental constitution in the two cases as follows :—

(i) *AB* *CD* (ii) *AB* *BC*
BC *DA* *AB* *BC*
BC *DA* . . . *AB* *BC* . . .

Either type can form three pairs instead of the expected two trivalents.

Since all the triploids in which this behaviour is found are interspecific hybrids of *ABC* or *AAB* types (*cf.* Ch. VIII), or, in *Festuca*, *Œnothera* and *Campanula*, the offspring of interchange heterozygotes, the heterozygote rather than the homozygote explanation is favoured. Homozygous reduplication may also have contributed to the result in some cases.

A clearly defined heterozygote is the triploid derived from

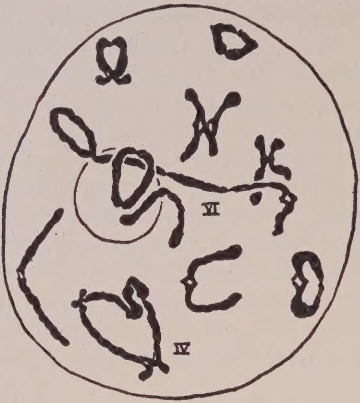


FIG. 45.—Diakinesis in *Rosa relicta* ($4x = 28$) with one association of six and one ring of four. × 4500 (from Erlanson, 1931).

Œnothera pycnocarpa. The parent has a ring of 14 chromosomes which are presumably of the segmental constitution :

AB *CD* *EF* *GH* *KL* *MN* *OP*
\ / \ / \ / \ / \ / \ / \
BC *DE* *FG* *HK* *LM* *NO* *PA*

the upper row of chromosomes being derived from one gamete, the lower from the other.

The fertilisation of an unreduced gamete (with the constitution of the zygote) by a normal gamete has given a triploid of the constitution :—

AB *CD* *EF*
AB *CD* *EF*
BC *DE* *FG*, etc.

This gives all the expected small configurations (like those in the tertiary trisomic *Datura*), but none with the maximum association (including all 21 chromosomes), since this would involve the apparently unlikely chance of 14 of the chromosomes forming two chiasmata in each arm (Catcheside, 1931 *a*).

Several tetraploid species show by their pairing that they are interchange heterozygotes, but for the reasons stated above an exact constitutional formula cannot be given with certainty. In these tetraploids an association of more than four chromosomes indicates that the plant is heterozygous for one interchange, and an association of more than eight or two of more than four, but not more than eight, indicates that the plant is heterozygous for two interchanges, and so on. The following table shows the percentages of configurations with different numbers of chromosomes in three such tetraploid species. It will be noticed that occasional unpaired chromosomes are characteristic of the polyploid as of the diploid interchange heterozygote.

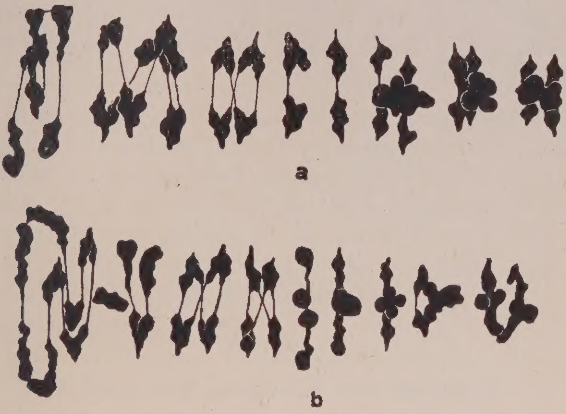


FIG. 46.—First metaphase in *Aucuba japonica* pollen mother-cells ($4x = 32$). *a*, two sixes, four fours, and two pairs. *b*, one eight, three fours, one three, four pairs, and one unpaired chromosome. × 2400. (From Meurman, 1929.)

TABLE 19

Pairing in Tetraploid Interchange Heterozygotes

Configurations.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.
Anthoxanthum odoratum ($x = 5$). Kattermann, 1931 (1120 chrs.).	5·8	59·9	2·4	20·4	0·7	4·8	0·0	3·8	0·0	1·4	0·0	1·4
Rosa relicta ($x = 7$). Erlanson, 1931 (380 chrs.).	1	62	3	23	2	2	2	5	0	0	0	0
Aucuba japonica ($x=8$). Meurman, 1929 *a* (2496 chrs).	0·3	34·9	0·8	52·7	0·1	5·2	0·1	4·8	0·1	0·8	0	0

Similar behaviour is found in *Tradescantia virginiana* (Stow, 1928 ; D., 1929 *c*) and *Campanula persicifolia* (Gairdner and D., 1931), in which forms of various constitutions probably occur. The constitution of the tetraploid forms of *Œnothera* can be specified from knowledge of the behaviour of the diploids from which they are derived, and they show the types of configuration that are to be expected on these grounds (Håkansson, 1926 ; Catcheside, 1932).

TABLE 20

Classification of Interchange Heterozygotes

(*a*) DIPLOIDS.

Artificial Hybrids.

*Datura** ($n = 12$) . .	Blakeslee, 1928, 1929.
Pisum ($n = 7$) . .	Håkansson, 1929, 1931. Richardson, 1929. E. R. Sansome, 1932.
Polemonium reptans (race cross) . . .	J. Clausen, 1931 *a*.
P. mexicanum × *P. pauciflorum* . .	
P. filicinum × *P. cæruleum*	—
*Canna** . . .	Honing, 1928.

---

* Chiasmata all terminal apart from those arrested by change of homology, *cf.* p. 321. Numbers in brackets are the numbers of chromosomes in a ring.

Godetia amœna ($n = 7$) × *G. Whitneyi** ($n = 7$) .	Håkansson, 1925, 1931 *b*.
*Œnothera** (4) and (6) .	Gates and Catcheside, 1931.
Drosophila melanogaster (X-rayed) . . .	Muller, 1930.
Spontaneous Forms.	
*Campanula persicifolia** ($n = 8$) (4) and (6) .	Gairdner and D., 1931.
Œnothera spp.* ($n = 7$) (14)	Cleland, 1922–27 ; D., 1931 *c*.
*Rhœo discolor** ($n = 6$) (12)	Belling, 1927 ; D., 1929, *a* and *c* ; Kato, 1929 ; Sax, 1931 ; Koller, 1932 *c*.
*Humulus japonicus** ♂ .	Kihara, 1929 *b* (*v.* sex chromosomes).
*H. lupulus** ♂ . .	Sinoto, 1930 (*v.* sex chromosomes).
*Briza media** . . .	Kattermann, 1930, 1931.
Zea Mays (in experiment) (4) and (6). . .	Burnham, 1930 ; McClintock, 1931.
*Eucharidium concinnum** .	Schwemmle, 1926.
*Clarkia elegans** ($n = 9$), 2 plants (4) + 7 (2) .	Håkansson, 1931 *b*.
Polemonium cæruleum .	J. Clausen, 1931 *a*.
*Hypericum punctatum** ($n = 8$) (16) . .	Hoar, 1931.
Matthiola incana ($n = 7$) .	Philp and Huskins, 1931.
Rosa forms ($n = 7$) . .	Erlanson, 1931 *b*.
Trimerotropis citrina Orthoptera ($n = 12$) .	Carothers, 1931.

(*b*) TRIPLOIDS.

Zea Mays (10) × *Euchlæna perennis* (20), $2^{III} + 10^{II} + 8^{I}$. Longley, 1924.

Artemisia nitida ($3x = 27$), $9–13^{II}$. Chiarugi, 1926 ; *cf.* Rosenberg on *Hieracium*, 1917, and Ch. XV.

Ægilops ovata (14) × *Æ. caudata* (7), $7–10^{II}$. Bleier, 1927.

---

* Chiasmata all terminal apart from those arrested by change of homology, *cf.* Ch. XII. Numbers in brackets are the numbers of chromosomes in a ring.

Ægilops speltoides (7) × *Triticum turgidum* (14). Jenkins, 1929.

Bivalents . .	4	5	6	7	8	9	10
Frequency . .	1	5	9	71	15	1	1

Avena barbata (14) × *A. strigosa*, $9^{\mathrm{II}} + 3^{\mathrm{I}}$. Nishiyama, 1929 (N.B. lateral chiasma).

Triticum ægilopoides (7) × *T. dicoccum* (14), $1^{\mathrm{IV}} + 1^{\mathrm{III}} + 4^{\mathrm{II}} + 6^{\mathrm{I}}$. Kihara and Nishiyama, 1930.

Fragaria bracteata vesca (14) × *F. collina* (7), 10^{II}, etc. Yarnell, 1931 *b*.

Œnothera pycnocarpa ($3x = 21$) (see text). Catcheside, 1931.

Campanula persicifolia ($3x = 24$), $1^{\mathrm{IV}} + 4^{\mathrm{III}} + 3^{\mathrm{II}} + 2^{\mathrm{I}}$. Gairdner and D., 1931.

[*Festuca pratensis* (7) × *Lolium perenne* (7)] × *L. perenne* ($3x = 21$), 3^{III}, 6^{II}, etc. Peto, 1932.

(*c*) TETRAPLOIDS.

Tradescantia virginiana ($x = 6$) . . .	D., 1929 *c*.
Campanula persicifolia ($x = 8$) . . .	Gairdner and D., 1931.
Aucuba japonica ($x = 8$) .	Meurman, 1929 *b*.
Rosa relicta ($x = 7$) .	Erlanson, 1931 *b*.
Œnothera Lamarckiana ($x = 7$) . . .	Håkansson, 1927.
Anthoxanthum odoratum ($x = 5$) . . .	Kattermann, 1931 ; *cf.* Avdoulov, 1931.

(*d*) HEXAPLOID.

Rumex acetosella ($x = 7$) (association of 8) .	Kihara, 1927.

In *Pisum* and *Œnothera*, plants have been found which are both interchange and translocation heterozygotes. These will be considered in their special relationship to the theory of crossing-over (Ch. X).

(vii) Unequal Pairs of Chromosomes. In accordance with the foregoing classification of structural hybrids it is possible to distinguish provisionally between four kinds of condition which give rise to the occurrence of unequal pairs of chromosomes at meiosis.

TABLE 21

Classification of Unequal Bivalents

1. DEFICIENCY, REDUPLICATION OR TRANSLOCATION HETEROZYGOTES.	
Forficula auricularia	Payne, 1914. W. P. Morgan, 1928
Brachystola *Arphia* *Dissosteira*	Carothers, 1913.
Phrynotettix magnus	Wenrich, 1916.
Acridium	Robertson, 1915.
Circotettix verruculatus	Carothers, 1931 ; Helwig, 1929.
Mus musculus (mutant)	Painter, 1927 (deficiency).
Labidura bidens	W. P. Morgan, 1928.
Mecostethus gracilis	McClung, 1928 *b*.
Stenobothrus lineatus	Belar, 1929 *a*.
Ribes hybrids	Meurman, 1928.
Vicia hybrids	Sveshnikova, 1929.
Ægilops ovata × *Triticum polonicum* (4*n*)	Kagawa, 1929.
Æ. cylindrica × *Æ. triuncialis* (4*x*)	Kagawa, 1931.
Bougainvillæa glabra	Cooper, 1931.
Zebrina pendula (4*x*)	D., 1929 *c*.
Crepis hybrids	Babcock and J. Clausen, 1930.
Aloë purpurascens	Belling, 1931 (lateral chiasma).
2. FRAGMENTATION HETEROZYGOTES.	
Vicia sativa × *V. amphicarpa*	Sveshnikova, 1929.
Tradescantia virginiana	D., 1929 *c*.
Crepis leontodontoides × *C. marschalli* (4*x*), etc.	Avery, 1930 (Fig. 47).

3. INTERCHANGE HETEROZYGOTES.

Œnothera biennis	D., 1931 *d*.
Tradescantia virginiana	D., 1929 *c*.
Anthoxanthum odoratum	Kattermann, 1931.
Orgyia thyellina × *O. antiqua*	Cretschmar, 1928.

4. COMPLEX AND SEX HETEROZYGOTES (*v.* Ch. XIV).

The differences between these chromosomes can be accounted for by the assumption of simple structural changes in a way that will explain their behaviour at meiosis. Translocation, for example, affords a simple explanation where, as in *Circotettix*, there is a difference in position of the spindle attachment without difference of size. But it is probable, more especially in species hybrids, that numerous structural differences distinguish the chromosomes. This is clear in the hybrids of *Lycia zonaria* ($n = 56$) by *L. hirtaria* ($n=14$) (Harrison and Doncaster, 1914), *Lycia pomonaria* ($n = 51$) by *L. hirtaria* ($n = 14$) (Malan, 1918), and *Orgyia thyellina* ($n = 11$) by *O. antiqua* ($n = 14$). In each cross the chromosomes of one species are smaller and more numerous than those of the other.

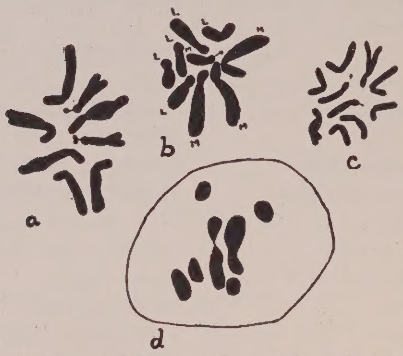


FIG. 47.—*a*, *Crepis marschalli*, $2n = 8$. *c*, *C. leontodontoides*, $2n = 10$. *b*, the hybrid at mitosis. *d*, the hybrid at first metaphase ; two unequal pairs and five unpaired chromosomes. × 1800. (*a* and *c* from Babcock and Navashin, 1929 ; *b* and *d* from Avery, 1930.)

Fragmentation or fusion is therefore to be inferred. But in the *Orgyia* hybrid not only associations of three (as in *Phragmatobia*) but also of larger numbers are found. Their details cannot be made out, but interchange or translocation is to be inferred. In a *Dicranura* hybrid definite chains can be made out (Federley, 1915). Closer study of many hybrids amongst those that will be classified as "undefined" would probably reveal analogous results and make it possible to specify some of the differences that constitute their hybridity.

There is another class of hybrids that may be considered structural hybrids, on account of the formation of chains of chromosomes at meiosis, but in which the possibility has not been eliminated of these being the multivalents characteristic of many polyploid hybrids. Such are a series of *Viola* hybrids in which interchange has been inferred (J. Clausen, 1931 *c*). Extensive studies of each hybrid and its parents are necessary to distinguish between the fixed configurations of an interchange heterozygote and the variable configurations of a polysomic organism. It is not yet known whether the sets in *Viola* of 10, 11, 12 and 13 chromosomes are related to the 7 set through fragmentation or reduplication, although the latter is more probable. Thus the occurrence of an association of 4 chromosomes at meiosis in a cross between species of 13 and 17 chromosomes, or between two species with 17 chromosomes (*v.* Table 28), may indicate interchange hybridity in a diploid or polysomy. In the latter case the species are probably secondary polyploids (*q.v.*).

CHAPTER VI

MEIOSIS IN UNDEFINED HYBRIDS

Conditions of Chromosome Pairing—Pairing in Undefined Hybrids—Classified Observations—Behaviour of Unpaired Chromosomes.

1. THE CONDITIONS OF CHROMOSOME PAIRING

BEFORE turning to more complicated kinds of hybrids we shall do well to consider how far observations of simpler kinds will help us. These show the following conditions of chromosome pairing.

(*a*) Where the chromosomes of a diploid organism can be seen at mitosis to consist of different pairs of identical chromosomes, the chromosomes associated in pairs at meiosis are always seen to be identical. Since the pairs segregate at random with regard to one another their members must be identical chromosomes and pairing must be a criterion of their common ancestry, that is, of their homology (Montgomery and Sutton). This conclusion is borne out by the usual absence of pairing in haploid plants (Ch. XIII).

(*b*) In tetraploids, as also in triploids, pairing takes place between corresponding parts of the pairing chromosomes at random, so that the chromosomes often change partner. Pairing is therefore not a property of the chromosome as a whole but of its constituent parts, and parts of chromosomes in structural hybrids pair according to their individual similarities with parts of other chromosomes.

(*c*) The pairing of chromosomes is subject to the conditions of meiosis being normal, and these conditions can be modified by genetic factors, the abnormal factor being recessive in the known cases (Ch. XIII).

It follows that failure is not in itself evidence of dissimilarity of the chromosomes concerned, although pairing is evidence of similarity.

(*d*) Likewise, genetic conditions may determine a failure to pair of *particular* members of the complement (as in the microchromosomes of Hemiptera, *v.* Ch. XIII), or of certain parts of the chromosomes (as in the distal parts of the chromosomes of *Mecostethus*). Such failure is certainly not the consequence of dissimilarity, because these chromosomes and parts of chromosomes are inherited in the same way as the rest of the complement.

(*e*) It has been seen that, while pachytene pairing is the first visible condition, chiasma formation is to be regarded as a second and immediate condition of the pairing of chromosomes. Therefore the interpretation of chromosome pairing in hybrids must take into account the frequency and distribution of chiasmata in the parent. First, pairing in a hybrid of a type with localised chiasmata will be dependent on the identity of the parts in which the chiasmata are formed, and trivalents in a triploid will be less frequent if chiasmata are localised. This has not yet been proved. Secondly, proportionate dissimilarities will reduce pairing more considerably in a type with low than in one with high chiasma frequency, a respect in which races of *Fritillaria imperialis* differ (*cf.* Ch. V), and in short chromosomes more than in long ones. Thirdly, where pairing fails it will vary in the extent of its failure in different nuclei, following a unimodal curve such as that found in trivalent formation and in chiasma frequency itself. It will also show variation in different individuals from other conditions affecting chiasma frequency (*cf.* Ch. X and Fig. 48).

(*f*) The occurrence of interlocking and its origin as shown by Gelei (*v.* Ch. X) and the occurrence of exchanges of partner at zygotene in polyploids (D., 1929 *c*) indicate that the accidents of relative position may reduce the completeness of pairing. These observations apply equally to pairing in translocation-heterozygotes, for the same exchanges of partner occur optionally amongst the homologous chromatids of non-hybrid polyploids as occur necessarily amongst the interchanged chromosomes of the heterozygotes. It is therefore not surprising to find in certain polyploids a considerable reduction of chiasmata, and, with terminalisation, many more free ends than in the corresponding diploids. This is increasingly evident in the series: *Datura Stramonium* (Belling, 1927), *Primula sinensis* (D., 1931 *a*), *Tradescantia virginiana* (D., 1929 *c*), *Campanula persicifolia* (Gairdner and D., 1931).

Interference of one chromosome with another at zygotene is greater in its effect on the longer chromosomes. Thus in triploid *Hyacinthus* the long chromosome type has a much wider variation in the length paired at zygotene than the short and medium chromosomes. It pairs as though it consisted of only two blocks which pair, or do not pair, at random with regard to one another. It therefore has a higher proportion of unpaired chromosomes at metaphase than the medium type, in spite of its higher chiasma frequency (*v.* Ch. IV).

In hybrids with some polarisation of the nucleus at zygotene, interference with pairing from structural hybridity will give an advantage to the ends of the chromosomes (which pair first) in pairing, and chiasmata will be formed chiefly near the ends. This is probably responsible for an increase in the frequency of terminal association in *Triticum* hybrids in proportion to the reduction in frequency of pairing (*cf.* D., 1930 *c*). The terminal association is always described as " loose " pairing in contradistinction to " close " pairing where the pairs have formed several interstitial chiasmata. It is directly determined by the formation of fewer chiasmata, nearer the ends than usual (Kihara and Nishiyama, 1930 ; *cf.* D., 1931 *d*).

These considerations are closely paralleled by observations of crossing-over in structural hybrids of various kinds (Ch. XI).

Summing up : The foregoing observations show three general conditions of the pairing of chromosomes at metaphase of the first meiotic division in diploids, as follows :—

(i) The presence of similar pairs of chromosomes.

(ii) Genetic and environmental conditions permitting their pairing at pachytene.

(iii) Genetic and environmental conditions permitting the formation of chiasmata in the paired pachytene chromosomes.

In polyploids the pairing of a particular two similar chromosomes depends on a combination of the chance of assortment of them, determined by the number of pairing blocks of which they consist, and the chance of chiasma formation determined by the average chiasma frequency and the interference value.

Two questions then arise : (*a*) What kinds of dissimilarity inhibit or restrict chromosome pairing at pachytene ? (*b*) What relation has metaphase pairing (which can alone be considered in detail) to the degree of dissimilarity occurring ?

(*a*) There is evidence of two kinds of dissimilarity or differentiation in the chromatin material. First, there is a qualitative differentiation between particles or groups of particles. This is most simply supposed to be due to differences between their characteristic molecules. A second symptom of these differences is the capacity for specific variation, the property of particles at each locus in a chromosome giving rise to differences (mutations) of a specific character, which has led to such an identifiable particle being described as a " gene." It is probably through gene mutations that the qualitative (intramolecular) differentiation arises. Secondly, there are differences due to change in arrangement or structure of these specific particles ; these intermolecular changes determine genetic differences when they lead to changes in quantity, proportion, and, possibly, position.

Since intramolecular changes affect single molecules and intergenic changes affect larger or smaller groups of genes (perhaps many hundreds), though both may inhibit pairing (on the simple assumption that only identical genes may pair), the first will have a negligible effect as compared with the second. Therefore the assumption will be made that all changes effective in reducing pairing, apart from changes of number, are intergenic or structural.

Structural changes need not in themselves mean any change of genetical properties in the organism, except in a mechanical sense, since the same materials may be arranged in a different way without any phenotypic effect. But structural changes will nearly always lead to changes in proportion through recombination, and these have an important genetic significance. Their occurrence is therefore a measure of differentiation.

(*b*) Since organisms vary (within and between species) in the frequency and distribution of chiasmata in each unit of the length of paired chromosome, it follows that the pairing in different hybrids between species and between varieties of the same species cannot be compared as an indication of similarity without a knowledge of chiasma frequencies in the parents.

We are therefore led to expect that, in some hybrids between species, chromosomes will pair, in others, they will fail to pair, and, in others again, their behaviour will be intermediate and will then vary in accordance with the variation in chiasma formation. The differences of behaviour between hybrids will have a very indirect relation to the differentiation in genetic properties of the parent species.

2. CHROMOSOME PAIRING IN UNDEFINED HYBRIDS

Undefined hybrids in which parental gametes have the same chromosome number, or a slightly different one, for no definable reason, are of three kinds : (i) those with little or no pairing at metaphase ; (ii) those with partial, and, always, variable pairing ; (iii) those with complete or almost complete pairing (*v*. Table 22). Prophase conditions have not been suitable for exact study in most of these hybrids, but failure of metaphase pairing has frequently been found to follow incomplete pachytene pairing, as would be expected (*cf.* Cretschmar, 1927). In other cases pairing appears to be complete at pachytene (Federley, 1915), but it may well be intermittent and appear complete as in *Fritillaria Meleagris*.

The second class is characterised by a unimodal curve in the frequency of the pairing (*v*. Table 23). This curve shows some variation even between different preparations of the same individual, but particularly in sister individuals from the same cross. Such variation is paralleled by that found in chiasma frequencies shown by the same chromosome pair in different preparations in non-hybrids (*cf.* D., 1931 *c*, on Maeda, 1930, *cf.* Fig. 48).

In the second and third classes it is also found that wherever the chiasma frequency of the parents is known or can be inferred, it is found to be lower in the hybrid. Thus in *Canna, Triticum* and *Papaver* two or three chiasmata are formed by the bivalents in the parental species ; the chromosomes are then said to be closely paired (*cf.* Table 24, and Peto, 1932). But in hybrids in these genera or between *Triticum* and *Ægilops*, where the pairing is small and variable, such pairing as occurs is by single (usually terminal or sub-terminal) chiasmata. The chromosomes are then said to be " loosely " paired (Figs. 49 and 58).

It will be observed that the difference between the two degrees of pairing is the same as that observed between the pairing of fragments which only form one chiasma and their large sister chromosomes which form two or more (*e.g.*, in *Fritillaria*, D., 1930 *c*, and *Datura*, Blakeslee, 1931). The pairing found in undefined hybrids is therefore in accordance with the assumption that a larger or smaller fraction of the total length of chromosome threads is paired at pachytene ; a small reduction leading to rare failure of chiasma formation and metaphase pairing ; a larger reduction, to more frequent but variable failure of pairing ; and a very large reduction to almost invariable failure of pairing. The conditions that determine this reduction are clear from the genetical and cytological evidence of the conditions of pairing just considered. It is that corresponding chromosomes do not agree in structure.

Where the differences between pairing chromosomes are sharp the result is recognisable and the hybrid can be classified as a structural hybrid. Where the differences depend on change in small segments, they are just as important, but they will not be revealed by cytological observation and the hybrid may be spoken of as an undefined hybrid. This conclusion is confirmed by the observations of differential affinity to be considered later (Ch. VII).

If mere differences in the arrangement of the same materials are responsible for failure of pairing (and these differences do not in themselves imply differences in the genetic properties of the chromosome set) then frequency of pairing at pachytene is an uncertain indication of the genetic relationship of the parents. And since metaphase pairing is related to pachytene pairing through the formation of chiasmata, in the frequency of which species and varieties differ genetically, the indication becomes even more uncertain. This conclusion is verified by a consideration of chromosome pairing in hybrid Lepidoptera (*cf.* Cretschmar, 1927). The different behaviour of the chromosomes of *Digitalis lutea* and *Chrysanthemum marginatum* (*v.* Table 28) in different hybrids is, as will be seen, in agreement with this anticipation. Under different genetical conditions the same pairs of chromosomes do not unite (Ch. XIII).

Finally when, as in polyploid hybrids, pairing is seen to be governed by "differential affinity" (Ch. VII), deductions from pairing must have an enormous margin of error. The extensive phylogenetic conclusions that have been based on observation of pairing in hybrids, especially in *Triticum* and *Nicotiana,* must therefore be regarded as provisional.

The results of defective pairing in undefined hybrids are indistinguishable from those in numerical and structural hybrids (*cf.* Chs. IV and XIII).

TABLE 22

CLASSIFIED OBSERVATIONS OF PAIRING OF CHROMOSOMES IN UNDEFINED HYBRIDS

The haploid number is given after each species, and the number of pairs (x^{II}) formed by the hybrid where this is variable.

(1) **Potentially Complete Pairing.**

Oporabia filigrammaria (37) × *O. autumnata* (38), 34–37$^{\text{II}}$. Harrison, 1920 *a.*

Pergesa porcellus (29) × *P. elpenor* (29). Federley, *cit.* Cretschmar, 1927.

Amorpha populi austauti (28) × *A. p. populi* (28). Federley, *cit.* Cretschmar, 1927.

Celeris euphorbiæ (29) × *C. galii* (29). Bytinski Salz and Günther, 1930.

Primula floribunda (9) × *P. verticillata* (9) (= *P. kewensis*). Digby and Pellew, 1914; *cf.* Newton and Pellew, 1929.

Digitalis lanata (28) × *D. micrantha* (28). Haase-Bessel, 1922.

Tragopogon pratense (6) × *T. porrifolius* (6)
Geum rivale (21) × *G. urbanum* (21).
} Winge, *cit.* Babcock and J. Clausen, 1929.

Prunus persica (8) × *P. Amygdalus* (8)
P. triflora (8) × *P. persica* (8).
P. triflora (8) × *P. cerasifera* (8)
} D., 1930 *a.*

Fragaria vesca (7) × *F. Helleri* (7)
F. bracteata (7) × *F. Helleri* (7)
F. glauca (28) × *F. virginiana* (28)
} Ichijima, 1926.

Sorbus Aria (17) × *Aronia melanocarpa* (17). Sax, 1929.

Ribes rubrum (8) × *R. petræum* (8) (= *R. holosericeum*). Meurman, 1928.

Viola tricolor (13) × *V. alpestris* (13) } J. Clausen, 1931 *c.*
V. cornuta (11) × *V. orthoceras* (11) }

Salix viminalis (19) × *S. Caprea* (19). Håkansson, 1929 *b.*

Crepis rubra (5) × *C. fœtida* (5). Poole, 1931.

C. leontodontoides (5) × *C. aurea* (5). Avery, 1930.

Triticum dicoccum (14) × *T. persicum* (14). Vakar, 1929.

T. durum (14) × *T. turgidum* (14). D., 1931 *d* (*v.* Table 24).

Lolium perenne (7) × *Festuca elatior* (7). Peto, 1932 (*v.* Ch. XIII).

(2) **Partial Pairing** (always variable).

Saturnia pyri (30) × *S. pavonia* (29), 5–6ᴵᴵ. Pariser, 1927.

Smerinthus ocellata ocellata (27) × *S.o. planus* (27), 5–18ᴵᴵ. Federley, 1913, 1914.

Crepis hybrids (4, etc.), 0–4ᴵᴵ. Babcock and J. Clausen, 1929 (*v.* Table 23); Avery, 1930.

Papaver somniferum glabrum (11) × *P. nudicaule* (7), 3–4ᴵᴵ. Yasui, 1927.

Ribes sanguineum (8) × *R. Grossularia* (8) ("*R. Gordonianum*"), 0–8ᴵᴵ. Meurman, 1928.

R. nigrum (8) × *R. Grossularia* (8) ("*R. Culverwellii*"), 0–8ᴵᴵ. Meurman, 1928.

Digitalis purpurea (28) × *D. ambigua* (28), 5–12ᴵᴵ. Buxton and Newton, 1928.

Viola arvensis (17) × *V. rothomagensis* (17). 14–15ᴵᴵ. J. Clausen, 1931 *c.*

V. nana (24) × *V. lutea* (24), 15–17ᴵᴵ. J. Clausen, 1931 *c.*

Ægilops cylindrica (14) × *Æ. ovata* (14), 7–13ᴵᴵ. Percival, 1930.

Æ. cylindrica (14) × *Æ. triuncialis* (14), 6–11ᴵᴵ. Kagawa, 1931.

(3) **Potentially Complete Failure of Pairing.**

Pygæra anachoreta (30) × *P. curtula* (29), 0–2ᴵᴵ } Federley, 1913.
P. pigra (23) × *P. curtula* (29), 0–2ᴵᴵ }

Oporabia dilutata (30) × *O. autumnata* (38). Harrison, 1920 *a.*

Raphanus sativus (9) × *Brassica oleracea* (9), 0–1ᴵᴵ. Karpechenko, 1927, *a* and *b.*

Nicotiana Bigelovii (24) × *N. suaveolens* (16), 0–1$^{\text{II}}$. Goodspeed and Clausen, 1927 *a*.

Populus Simonii (19) (presumed hybrid, male), 0–1$^{\text{II}}$. Meurman, 1925.

Digitalis lutea (56) × *D. purpurea* (28). Haase-Bessel, 1916.

Canna (9) (presumed hybrid), 0–3$^{\text{II}}$. Belling, 1927.

Triticum dicoccoides (14) × *Ægilops ovata* (14), 0–5$^{\text{II}}$. Kihara, 1929 *a*.

TABLE 23

The Fluctuation of Chromosome Pairing in Hybrids

	Percentage of Cells.									Total Number of Observations.
	0^{II}	1^{II}	2^{II}	3^{II}	4^{II}	5^{II}	6^{II}			
Crepis spp. ($n = 4$). Babcock and J. Clausen, 1929.										
C. aspera × *C. bursifolia*	18	42	18	14	9	—	—			59
C. taraxacifolia × *C. tectórum*	30	27	37	6	0	—	—			30
C. aspera × *C. aculeata*	61	31	8	0	0	—	—			36
Triticum and *Ægilops* spp. ($n = 14$).										
(i) Kagawa, 1929.										
Æ. cylindrica × *T. dicoccum*	76	22	2	1	0	0	0			118
(ii) Kihara, 1929 *a*.										
T. dicoccoides × *Ægilops ovata* (different florets) (*a*)	2	24	28	31	15	0	0			100
(*b*)	2	22	26	22	24	2	2			50
(*c*)	68	26	6	0	0	0	0			50
(sister seedlings) (*d*)	73	23	4	0	0	0	0			100
(*e*)	1	18	36	27	11	6	1			100
(iii) Kihara, 1931.										
T. Spelta (21) × *Æ. triuncialis* (14) (different florets) (*a*)	7	28	41	13	8	3	0			100
(*b*)	56	34	6	3	1	0	0			100
	0^{II}	1^{II}	2^{II}	3^{II}	4^{II}	5^{II}	6^{II}	7^{II}	8^{II}	
Ribes spp. ($n=8$). Meurman, 1928.										
R. sanguineum × *R. odoratum* (different anthers) (*a*)	0	0	0	2	2	28	36	22	10	91
(*b*)	0	2	2	3	5	16	25	32	15	141
	23^{II}	24^{II}	25^{II}	26^{II}	27^{II}	28^{II}				
Amorpha populi austauti ($n=28$) × *A. p. populi* ($n = 28$). (Federley, 1915)	5	3	4	17	30	37				86

TABLE 24

Chiasma Frequency of Hybrids Compared with that of their Parents *

	Percentages of Bivalents with different Numbers of Chiasmata.				
	0	1	2	3	Mean.
Triticum, D., 1931 *d*.					
T. turgidum	—	—	57·1	42·9	2·43
T. durum	—	7·2	57·1	35·7	2·28
T. turgidum × *T. durum*	—	25·0	50·0	25·0	2·00
Kniphofia, Moffett, 1932.					
K. Nelsonii	0	30·8	56·7	12·5	1·8
K. Burchellii	0	42·4	54·6	3·0	1·6
K. Uvaria × *K. Macowanii*	2·6†	53·2	42·9	1·3	1·4

* *cf.* Peto, 1932, and Ch. XIII.
† Unpaired chromosomes.

3. THE BEHAVIOUR OF UNPAIRED CHROMOSOMES

Unpaired chromosomes have the same general type of behaviour whether in numerical, structural or undefined hybrids or organisms with genetically determined failure of pairing (*cf.* Ch. XIII). One description will therefore apply to all these cases.

Unpaired chromosomes usually lie at random on the spindle at metaphase. They do not move towards the equator like the paired chromosomes. Those that lie near the equatorial plate are no more attracted to it than those that lie further away. It is sometimes stated that unpaired chromosomes lying to one side of the plate are moving to the pole *in advance of* the bivalents at anaphase, but this conclusion is unjustifiable. Their position is due to their never having reached the plate, and they actually do not move until after the bivalents have divided.

When the paired chromosomes begin to separate at anaphase the unpaired chromosomes follow one of two courses: (i) those lying far away from the equator are included with the group of daughter bivalents passing to the nearest pole; (ii) those lying near the equator move on to the plate, orientate themselves axially, and divide after a short interval into their two chromatids, which then pass to opposite poles as in mitosis.

In *Triticum-Ægilops* hybrids Kihara (1931) in a detailed account has shown the probable history of the univalents to be entirely of the second type, which is as follows: (i) The bivalents arrange themselves on the equatorial plate; the univalents remain distributed at random. (ii) The univalents arrange themselves on the edge of the equatorial plate. (iii) The bivalents divide; the univalents remain on the equator. (iv) The univalents divide and their halves follow the daughter bivalents to the poles. The variations commonly observed in univalent behaviour are probably due to various degrees of delay in the movement of the univalents relative to those of the bivalents.

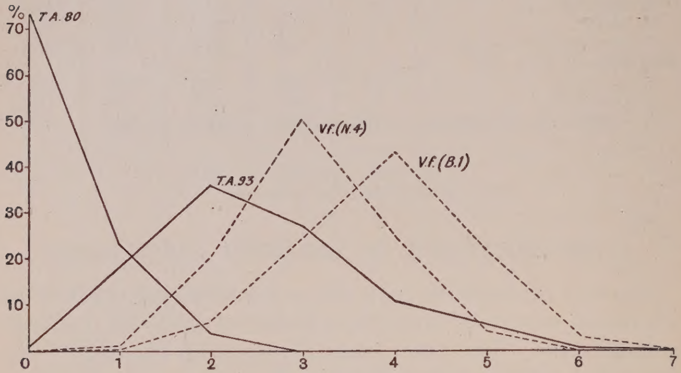


FIG. 48.—Percentage frequencies, *T.A.*, of chromosome pairing in a *Triticum-Ægilops* hybrid (Kihara, 1929 *c*) from different preparations and *V.f.* of chiasmata per bivalent in the *m* chromosomes of *Vicia Faba* (Maeda, 1930), also from different preparations showing the effect of different developmental conditions on these two variables. (From D., 1931 *c*.)

The daughter univalents usually lag at the second division or pass without division to one pole or the other. With division at either the first or the second division univalents are lost in the cytoplasm through failure to reach the poles. When they are present in large numbers they may determine the formation of

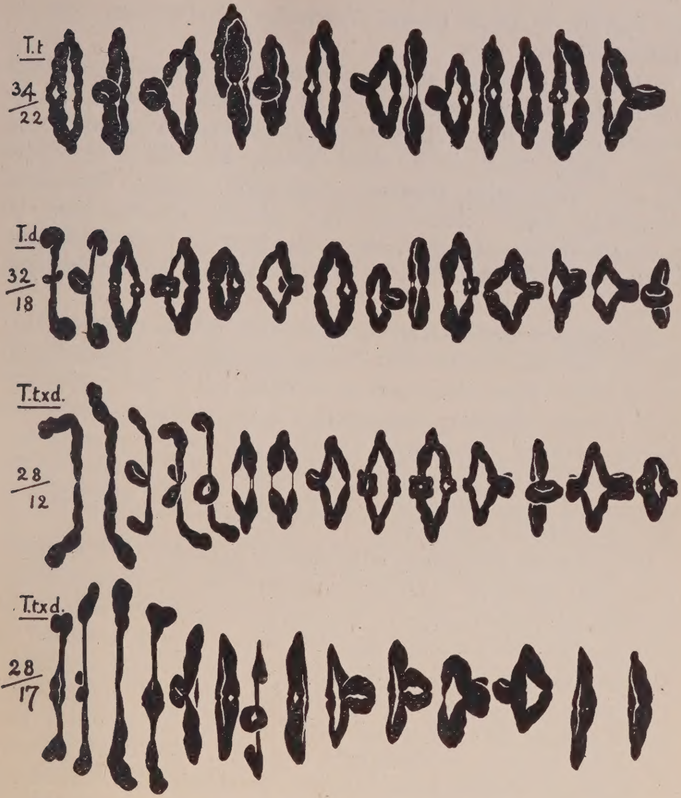


Fig. 49.—First metaphase of meiosis in *Triticum turgidum* ($2n = 28$), *T. durum* ($2n = 28$) and the hybrid between them. The total number of chiasmata and the number terminal is given at the side of each plate. *Cf.* Table 24, smear preparations: The top plate is fixed in aceto-carmine (× 1900), the rest in Flemming (× 2800). (From D., 1931 *d.* *Cf.* Fig. 58.)

"unreduced" gametes (*q.v.*), either through forming a bridge between the daughter-nuclei, which then form a single nucleus at the second division, or by dividing at both divisions.

Lagging chromosomes may be cut in two by the formation of the cell wall (D., 1929 *b*, in triploid *Hyacinthus* ; Kattermann, 1931, in *Anthoxanthum*).

Where all, or nearly all, the chromosomes are univalent their relationship to the spindle is often abnormal. Sometimes the nucleus relapses to a resting stage without any movement having taken place. This is a third means by which unreduced gametes may arise (*Papaver*, Ljungdahl, 1922 ; *Hieracium*, Rosenberg, 1927). Sometimes two separate spindles may be formed. This is not to be taken as due to the chromosomes being of two related groups (*cf.* Bleier, 1930) but as an accident of external cause.

Reviewing these observations we see that the chromosomes that lag are univalents at the first division and daughter univalents at the second. These chromosomes evidently fail to move, although they resemble the other chromosomes in every respect save in not having partners. Movement, therefore, depends on a reaction—presumably repulsion—of pairs of elements. The presence of the spindle and of the chromosome in the right position in relation to the spindle is not sufficient.

Why then are univalents, after more or less delay, able to divide at the first division ? And why is this division always preceded by an approach to the equator ? The simplest explanation seems to be that they undergo a change, that they become double or bipolar, in the organ determining, first the orientation, and then the separation. This organ is clearly the spindle attachment, and we are therefore led to suppose that the spindle attachment of the univalent does not divide until the bivalents have separated. The bearing of this on the theory of chromosome behaviour at meiosis will be considered later (Chs. XI and XII).

CHAPTER VII

THE BEHAVIOUR OF POLYPLOIDS

Autopolyploids and Allopolyploids—Origin in Experiment—Meiosis in Allopolyploids—Differential Affinity—Autosyndesis—Classification of Polyploid Species.

> The production of an indubitable sterile hybrid from completely fertile parents which have arisen under critical observation from a single common origin is the event for which we wait.
>
> BATESON, 1922.

1. THE ORIGIN OF POLYPLOIDS IN EXPERIMENT

A POLYPLOID is an organism with more than two complete *sets* of chromosomes (Ch. III). When the chromosome number is doubled in a homozygous diploid such as *Datura Stramonium*, the new organism has four *identical* sets of chromosomes. Such a form is known as an AUTOPOLYPLOID (Kihara and Ono, 1926). Its chromosome complement can be represented as of the constitution $A_1A_1A_1A_1$, $B_1B_1B_1B_1$, and so on. Its chromosomes have a high frequency of quadrivalent formation, subject to random chiasma formation amongst the four homologues of each kind (Ch. IV). Where the chiasma frequency is low, as in the short chromosomes of *Hyacinthus* and in some chromosomes of *Solanum* and *Primula*, bivalents are formed instead in a proportion of cells (*v. infra*).

In contradistinction to the autopolyploid, the product of doubling in hybrids is known as an ALLOPOLYPLOID. Its constitution may be represented as $A_1A_1A_2A_2$, $B_1B_1B_2B_2$, and so on. Such an allopolyploid is homozygous inasmuch as it may be derived immediately from the union of two genetically identical gametes; but it is also heterozygous inasmuch as its complement contains two, three or more dissimilar pairs of gametic sets. How this affects its behaviour we shall see later. But first we must make an arbitrary but convenient distinction between different kinds of allopolyploids. On the one hand, there are those derived from doubling in defined structural hybrids; where these are interchange heterozygotes pairing occurs between parts of structurally dissimilar chromosomes, and associations are formed correspondingly larger than those of the diploid (Ch. V). This group has been considered earlier because it agrees with autopolyploids in having no differentiation between the corresponding chromosomes such as seriously interferes with their pairing at meiosis.

On the other hand, the typical allopolyploids are derived from undefined hybrids; they show a gradation in behaviour from those with slight to those with strong differentiation between the homologues derived from opposite parents. At the extreme in one direction is such a hybrid as *Crepis rubra* × *C. fœtida* in which the difference between the parents is so slight that the diploid has complete pairing and the tetraploid derived from it behaves like an autopolyploid and occasionally forms five quadrivalents. In an intermediate position is the hybrid "*Primula kewensis*": in the diploid pairing is complete, but in the tetraploid derived from it only a small proportion of quadrivalents are formed. At the extreme in the other direction is *Raphanus-Brassica*. In the diploid no pairing occurs; in the tetraploid there are no quadrivalents; pairing is simple, complete and regular. Both the *Primula* and *Raphanus-Brassica* types breed approximately true and are highly fertile. They are, therefore, with a slight qualification functionally diploid. Frequently from crosses between such allotetraploids, through doubling again, octoploids have been produced, and from crosses with diploids the triploids resulting have given rise to hexaploids. These polyploids must be considered along with the original tetraploids both in regard to origin and behaviour. They may be, in relation to their immediate allopolyploid parents, themselves autotetraploid or allotetraploid. Thus the allohexaploid species, *Solanum nigrum* ($2n = 72$), yields an autotetraploid sport by doubling ($2n = 144$), while its pentaploid hybrid with *S. luteum* ($2n = 48$) gives an allotetraploid sport ($2n = 120$), which is, in relation to the basic number of the genus, a decaploid.

Chromosome Association in Polyploids

SPECIES

Datura Stramonium (12). Belling, 1927 ; $2x : 12^{\mathrm{II}}$; $4x : 12^{\mathrm{IV}}$.

Primula sinensis (12). D., 1931 *a* ; $2x : 12^{\mathrm{II}}$; $4x : 9\text{–}11^{\mathrm{IV}}$; $6 - 2^{\mathrm{II}}$.

Solanum Lycopersicum (12). Lesley, 1930 ; $2x : 12^{\mathrm{II}}$; $4x : 7 - 11^{\mathrm{IV}}, 10 - 2^{\mathrm{II}}$ (*cf.* Jørgensen, 1928).

UNDEFINED HYBRIDS

Crepis rubra × *C. fœtida* (5). Poole, 1931 ; $2x : 5^{\mathrm{II}}$; $4x : 0 - 5^{\mathrm{IV}}, 10 - 0^{\mathrm{II}}$.

Primula kewensis (9). (*P. floribunda* × *P. verticillata*.) Newton and Pellew, 1929 ; $2x : 9^{\mathrm{II}}$; $4x : 0 - 3^{\mathrm{IV}}, 18 - 12^{\mathrm{II}}$.

Triticum dicoccoides (14) × *Ægilops ovata* (14). Kihara and Nishiyama, 1931 ; $2x : 0 - 3^{\mathrm{II}}, 28 - 22^{\mathrm{I}}$; $4x : 0^{\mathrm{IV}}, 28^{\mathrm{II}}$.

Digitalis mertonensis (28). (*D. purpurea* × *D. ambigua*.) Buxton and Newton, 1928 ; $2x : 5 - 12^{\mathrm{II}}, 46 - 32^{\mathrm{I}}$; $4x : 0^{\mathrm{IV}}, 56^{\mathrm{II}}$.

Raphanus-Brassica (9). Karpechenko, 1927 ; $2x : 0^{\mathrm{II}}, 18^{\mathrm{I}}$; $4x : 0^{\mathrm{IV}}, 18^{\mathrm{II}}$.

The mechanically diploid behaviour of the allotetraploid means that the corresponding chromosomes that pair and pass to opposite poles to yield identical gametes, must always be those from the same parent and not those from opposite parents, even in tetraploids of the *Primula kewensis* type whose diploid parents show pairing of the homologues derived from opposite species. Such a difference in behaviour may be described as due to a " differential affinity " (D., 1928) whose significance in relation to prophase behaviour will be considered later.

In *Primula kewensis* the corresponding chromosomes of the diploid parents, *P. floribunda* and *P. verticillata*, are not sufficiently different to inhibit their pairing in the diploid hybrid. Such a lack of differentiation is associated with two abnormalities in the tetraploid : (i) Chromosomes of opposite parents occasionally pair (in quadrivalents or bivalents) and pass to opposite poles. The progeny therefore differ in the proportions of the chromosomes of the two species present. Moreover, owing presumably to this pairing being accompanied by crossing-over (Ch. X) the normal type can never again be recovered from its aberrant offspring. (ii) Quadrivalents are formed which sometimes divide unequally (as in the autotetraploid *Datura* and *Primula sinensis*), giving, therefore, gametes with 17 and 19 chromosomes instead of 18, and progeny with 34, 35 and 37 chromosomes instead of 36. These differ from the normal tetraploid both owing to a change in proportion within the set of nine and owing to a change in the proportionate influence of the two species. Such plants, particularly those with 34 chromosomes, which have 2 chromosomes of one type and 4 of the other 8 types, are less fertile than the normal tetraploid (*cf.* Ch. IX).

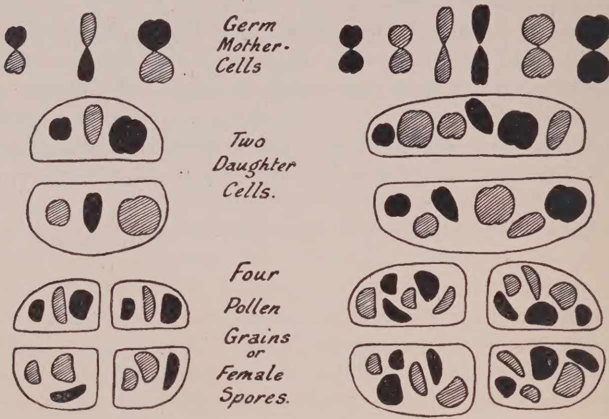


FIG. 50.—Diagram showing how chromosomes pair and segregate in a sterile diploid hybrid, such as *Primula kewensis*, and in the fertile tetraploid derived from it. The first gives various new (untested) combinations of chromosomes, the second gives uniformly the same combination that the parent had. (From D., 1932 *b*.)

The behaviour of plants derived from hybrids between species with different numbers (*e.g.*, diploid and tetraploid *Nicotiana*) may show a combination of the two extremes in the same nucleus.

Thus the *Nicotiana rustica-paniculata* hybrid is a triploid with 12 pairs and 12 univalents. Doubling, it gives rise to a hexaploid; this has two identical sets that pair with no other sets and therefore appear regularly as 12 bivalents, and it has four sets which form fluctuating numbers of quadrivalents and bivalents.

The sharp difference in chromosome behaviour between the allotetraploid and its hybrid parent causes a difference in fertility; this affords a means of determining the exact time and therefore mode of its origin, which would not otherwise be clear in all cases. The doubling of the chromosome number occurs in two ways: by failure of separation of two groups of chromosomes in a somatic mitosis (Ch. III) and by failure of such separation at one of the two meiotic divisions, giving in consequence "unreduced" gametes (Ch. XIII). Where the tetraploid arises by doubling in the somatic tissue of the first generation (F_1) hybrid, the affected shoot of this plant is as fertile as the progeny (F_2) it gives rise to, or even more so. Where it arises from failure of reduction in both germ-cells in the F_1 their successful union can only be occasional; the F_1 has therefore the characteristic sterility of hybrids and the F_2 is the first to regain full fertility (*cf.* Sansome, 1931). The contrast, it should be noted, is not so striking in the *Crepis* hybrid because it is not entirely sterile as a diploid; it gives diploid and triploid as well as tetraploid progeny. Further, it should be noted that frequent syndiploidy at the premeiotic divisions will be indistinguishable from failure of reduction.

TABLE 25

Fertility Showing the Origin of Polyploids after Hybridisation

1. Failure of Reduction (F_2 more fertile than F_1)

	Fertility of F_1.	Fertility of F_2.
Raphanus × *Brassica*, Karpechenko, 1927 *a*.	45 seeds per plant.	30 seeds per pod.
Digitalis purpurea × *D. ambigua*, Buxton and Newton, 1928.	200 seedings in two plants.	400 seeds per capsule.
Phleum pratense × *P. alpinum*, Gregor and Sansome, 1930.	11·5 seeds per plant.	400 seeds per plant.
Ægilotricum, Kihara and Katayama, 1931	27 ears gave 5 seedings.	61 per cent. fertile.
Crepis rubra × *C. fœtida*, Poole, 1931 .	50 seeds from 42 heads. 9 seedlings (3, $2x$; 5, $3x$; 1, $4x$),	55 seeds from 22 heads.

2. Somatic Doubling (F_2 of equal or reduced fertility).

Nicotiana glutinosa × *N. Tabacum*, Clausen and Goodspeed, 1925; Clausen, 1928.	155 seeds per fruit.	No greater.
Primula kewensis; *cf.* Sansome, 1931	30, 90 and 180 seeds per capsule. 287 germinated.	122 seedlings per capsule.
Solanum nigrum × *S. luteum*, Jørgensen, 1928.	8–11 seeds per capsule (*i.e.*, 25 percent.). ("Completely sterile" before doubling).	No greater.
Saxifraga rosacea × *S. granulata*, Whyte, 1930.	436 seeds per plant.	85 seeds per plant.

Hybrid polyploids that have arisen in experiment may be provisionally classified in accordance with these considerations, and with direct chromosome counts, as in Table 26.

(*Note on Table* 26. The female parent is given first. The numbers in brackets are the gametic numbers of the parents. In the first column are the somatic numbers of the offspring before doubling (F_1) and in the second column the numbers after doubling (F_1 or F_2). Where the failure of reduction occurs in the parent the first column is therefore blank. The initials in the second column represent the sets of chromosomes of parental species. Classes A to D show doubling of the contributions of both parents, classes E to H, of that of only one parent).

These observations show that allopolyploids have arisen in five ways. In the first, type *A*, a fertile shoot usually appears which is readily distinguishable in the otherwise sterile hybrid, but the doubling may occur so early in the development that, as in certain cases of haploid parthenogenesis (Ch. XV), the whole plant has the double number. In type *B*, the hybrid is usually highly sterile, but produces, here and there, viable seeds. In some hybrids a few of these seeds have the same chromosome number as their parent, or they result from doubling on one side only; they are relatively triploid (*e.g.*, in *Crepis* and *Nicotiana rustica-paniculata*). In these instances, the rest of the seedlings, and in other instances, all of them, have double the chromosome number of the parent; diploid gives tetraploid, triploid gives hexaploid, and so on. In type *C*, a triploid hybrid is produced through the fertilisation of an unreduced egg by a reduced pollen grain. This triploid, like most triploids, produces again an unreduced (triploid) egg which is fertilised by a reduced pollen grain of the second species again. In this way the doubling is achieved in two stages, which provide excellent illustrations of the difference in genetic effect of one and two sets of the species combined with two of the other (*e.g.*, in *Raphanus-Brassica* and *Rubus*).

In type *D*, a triploid arises in the same way. It has three pairs of *Crepis capillaris* chromosomes and four unpaired *C. tectorum* chromosomes. When selfed it produces a tetraploid, together with other products of the random segregation of the extra set of unpaired chromosomes. The reason why a tetraploid has arisen in this way in *Crepis* and not elsewhere is that only where the chromosome number is small will the triploid produce a moderate proportion of gametes having all the extra chromosomes, owing to their being distributed at random at meiosis (Ch. IX). Further, of the diploid gametes most are evidently eliminated ; since they should combine as frequently as haploids, yet only one tetraploid appeared in a family along with 59 diploids (Table 39).

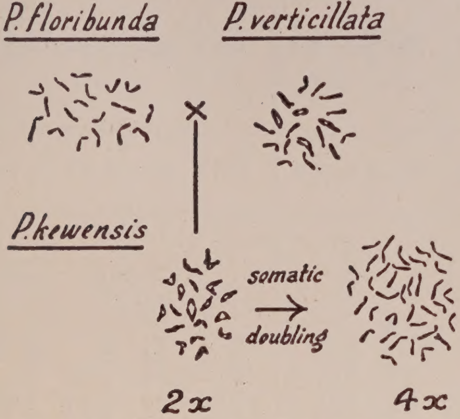


FIG. 51.—The origin of the tetraploid *Primula kewensis*, illustrated by drawings of mitotis ; the diploid hybrid and *P. verticillata* are in early anaphase. × 2500. (After Newton and Pellew, 1929.)

In type *E*, tetraploid and diploid species are crossed, and side by

TABLE 26

THE ORIGIN OF POLYPLOIDS IN EXPERIMENT

A. SOMATIC DOUBLING IN F_1.			
1. *Nicotiana glutinosa* (12) × *N. Tabacum* (24) ($2x + 4x = 6x$, " *N. digluta* ").	36	72	Goodspeed and Clausen, 1926: R. E. Clausen, 1928.
2. *Primula floribunda* (9) × *P. verticillata* (9) ($2x + 2x = 4x$, " *P. kewensis*," Fig. 51).	18	36	Newton and Pellew, 1928.
3. *Solanum nigrum* (36) × *S. luteum* (24) . . .	60	120	Jørgensen, 1928.
4. *Saxifraga rosacea* (16) × *S. granulata* (16) ($4x + 4x = 8x$, " *S. potternensis* ").	32	64	Whyte, 1930 (*cf.* Marsden-Jones and Turrill, 1930).
5. *Rubus strigosus* (7) × *R. rusticanus* (7) . . .	14	28	Crane and D., 1927.
6. *Brassica Napus* (18) × *B. campestris* (10). . . .	28	56	Frandsen and Winge, 1932.
B. GENETIC DOUBLING ON BOTH SIDES IN F_1.			
7. *Raphanus sativus* (9) × *Brassica oleracea* (9) . .	18	36	Karpechenko, 1927, *a*, *b*.
8. *Fragaria bracteata* (7) × *F. Helleri* (7). . . .	14	28	Ichijima, 1926.
9. *Ægilops ovata* (14) × *Triticum durum* (14) ($4x + 4x = 8x$, " *Ægilotricum* .")	28	56	Tschermak and Bleier, 1926.
10. *Ægilops ovata* (14) × *Triticum dicoccoides* (14) . .	28	56	
10a. *Triticum dicoccoides* (14) × *Ægilops ovata* (14) . .	28	56	Kihara and Katayama, 1930.
11. *Ægilops ovata* (14) × *Triticum turgidum* (14) . .	28	56	Percival, 1930.
12. *Triticum turgidum* (14) × *T. villosum* (7) . . .	21	42	Tschermak, 1930.
13. *Triticum vulgare* (21) × *Secale cereale* (7) . . .	28	56	Levitsky and Benetskaya, 1929.
14. *Triticum durum* (14) × *T. monococcum* (7)	21	42	Thompson, 1931.
15. *Phleum pratense* (7) × *P. alpinum* (14) . . .	21	4~~3~~2	Gregor and Sansome, 1930.
16. *Nicotiana Tabacum* (24) × *N. sylvestris* (12) . .	36	72	Rybin, 1929, 1931.
17. *Nicotiana paniculata* (12) × *N. rustica* (24) . . .	36	72	Lammerts, 1929, 1931; Goodspeed *et al.*, 1926.
18. *Digitalis purpurea* (28) × *D. ambigua* (8) ($8x + 8x = 16x$, " *D. mertonensis* ").	56	112	Buxton and Newton, 1928; *cf.* Buxton and D., 1932.
19. *Crepis rubra* (5) × *C. fœtida* (5)	10	20 (10 and 15 also)	Poole, 1931.

C. GAMETIC DOUBLING IN ONE PARENT AND IN F_1 (BACKCROSSED)			
20. [*Nicotiana Tabacum* (24) × *N. rustica* (24)] × *N. rustica*	—	(i) 72 (*TTR*) (ii) 96 (*TTRR*)	Eghis and Rybin, 1927.
21. [*Galeopsis pubescens* (8) × *G. speciosa* (8)] × *G. pubescens* ($2x + 2x = 4x$, " *G. pseudo-Tetrahit* ").	—	(i) 24 (*SSP*) (ii) 32 (*SSPP*)	Müntzing, 1930 *b*.
D. GAMETIC DOUBLING IN ONE PARENT FOLLOWED BY SEGREGATION.			
22. *Crepis capillaris* (3) × *C. tectorum* (4)	—	(i) 10 (*CCT*) (ii) 14 (*CCTT*)	Hollingshead, 1930 *b*.
E. DOUBLING IN POLLEN ONLY.			
23. *Euchlæna perennis* (20) × *Zea Mays* (10) . . .	—	40	Emerson and Beadle, 1930.
24. *Primula sinensis* (*) (24) × *P. sinensis* (12) . .	—	48	*Cf.* D., 1931 *a*.
F. DOUBLING IN EGG ONLY.			
25. *Saccharum officinarum* (40) × *S. spontaneum* (56) . .	—	136	Bremer, 1923.
26. *Rubus rusticanus* (7) × *R. thyrsiger* (14) . . .	—	28 ($4x$) (also 21, $3x$)	Crane and D., 1927.
27. *Rubus* " Loganberry " (21) × *R. idæus* (7) . . .	—	49 ($7x$)	Crane and D., 1927.
28. *Nicotiana Tabacum* (24) × *N. sylvestris* (12) .	—	60 ($5x$)	Webber, 1930.
29. [*Nicotiana Tabacum* (24) × *N. Rusbyi* (12)] × *N. sylvestris* (12).	—	48 ($4x$)	Brieger, 1931.
30. [*Nicotiana Tabacum* (24) × *N. Rusbyi* (12)] × *N. Tabacum* (24)	—	60 ($5x$)	Brieger, 1928.
31. *Campanula persicifolia** (8) × *C. persicifolia* (16) . .	—	32 ($4x$)	Gairdner and D., 1931.
32. [*Festuca pratensis* (7) × *Lolium perenne* (7)] × *Lolium perenne*	—	21 ($3x$)	Peto, 1932.
33. *Pygæra pigra* (23) × *P. pigra* (23) × *P. curtula* (29) .	—	75 ($3x$)	Federley, 1913, 1930.
34. *Dianthus sinesis* (30) × *D. Knappii* (15) . . .	—	60 ($4x$)	Andersson and Gairdner, 1931.
G. DOUBLING IN EGG OR POLLEN.			
35. *Salix viminalis* (19) × *S. Caprea* (19)	—	57 ($3x$)	Håkansson, 1929 *b*.
H. IRREGULAR DOUBLING IN EGG OR POLLEN.			
36. *Salix viminalis* (19) × *S. Caprea* (19)	—	84	Håkansson, 1929 *b*.
37. *Saturnia pavonia* (29) × [*S. pyri* (23) × *S. pavonia* (29)]	—	($3x$)	Pariser, 1927.

* Non-hybrids included here for convenience.

side with the expected triploid seedlings, tetraploids are found, differing from them in the preponderant influence of one parent and in greater fertility, although they are not simple allotetraploids. In the *Rubus* hybrid some quadrivalents are formed, as they were in its tetraploid parent, and genetic results show that the pairing in some types of chromosomes is between those derived from the same parent, and in others at random among the four homologues.

The increase in fertility in sterile diploids is in sharp contrast with the decrease which is always found in fertile diploids that double their chromosome number. In the following examples the tetraploid produced is less fertile than the diploid :—

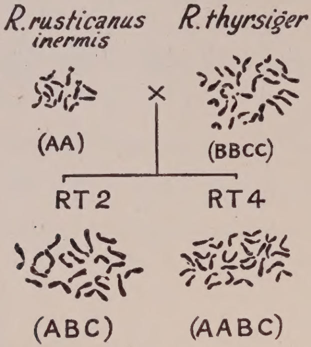


Fig. 52.—The origin of the tetraploid "RT4" and triploid "RT2" from a cross between two *Rubus* species, illustrated by mitotic metaphases. A, B and C represent sets of seven chromosomes. × 2000. (After Crane and D., 1927.)

Table 27

Autotetraploids with Reduced Fertility

Œ. Lamarckiana	*Cf.* Gates, 1928.
Datura Stramonium	Blakeslee *et al.*, 1923.
Primula sinensis	*Cf.* D., 1931 *a*.
Solanum nigrum	Jørgensen, 1928.
S. Lycopersicum	
Canna aureo-vittata	Honing, 1928.
Campanula persicifolia	Gairdner and D., 1931.

These are all autotetraploids except the structurally heterozygous *Œnothera*, which may be considered as an autopolyploid for this purpose, since, as has been seen, the differences between its homologues are so arranged as not to interfere with pairing.

Further, diploid hybrids of intermediate fertility give tetraploids of intermediate fertility, *e.g.*, in *Crepis* (Poole, 1931). It may therefore be said that there is an inverse correlation between the fertility of diploids and that of the tetraploids to which they give rise (D., 1928). The reason for this is evident. Two factors go to reduce generational fertility: (i) the segregation of dissimilar chromosomes (chiefly in the hybrid diploid); (ii) the unequal segregation of multivalents (chiefly in the autotetraploid). And the greater the dissimilarities in the diploid, the more regularly do the identical chromosomes pair in the allotetraploid derived from it, and therefore the less frequent are the multivalents in the tetraploid. Multivalents are invariably liable to segregate unequally (*e.g.*, *Datura*, Belling and Blakeslee, 1924; *Prunus*, D., 1928; *Primula*, D., 1931 *a*), and give rise to gametes and zygotes of reduced viability. The generalisation is therefore universally applicable subject to two qualifications :—

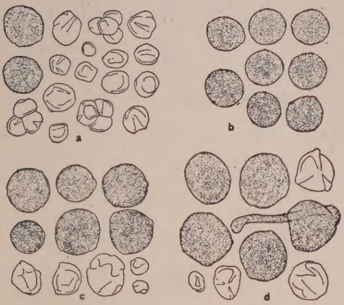


FIG. 53.

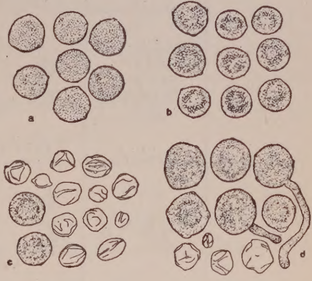


FIG. 54.

FIGS. 53 AND 54.—Pollen grains of *Solanum*. Fig. 53.—*S. nigrum* : *a*, *x* ; *b*, 2*x* ; *c*, 3*x* ; *d*, 4*x*. Fig. 54.—*a*, *S. nigrum* (2*x*). *b*, *S luteum*. *c*, the diploid hybrid. *d*, the tetraploid hybrid. × 160. (From Jørgensen, 1928.)

(*a*) The chromosomes must be capable of forming multivalents as they universally appear to be.

(*b*) The chromosomes of the haploid set must be numerous. *Crepis tectorum* with 4 chromosomes gives a relatively fertile tetraploid because the chance of unbalance is reduced.

(*c*) The chromosomes of each set must be qualitatively differentiated in a fairly high degree. This third condition is not applicable to high polyploids (such as *Rumex Hydrolapathum*, $2n = 200$; Kihara and Ono, 1926; and *Prunus Laurocerasus*, $2n = 180$; Meurman, 1929 *a*), nor apparently to *Hyacinthus orientalis*, for this species combines high fertility of the triploid with viability of unbalanced forms and lack of differentiation amongst them (D., 1929 *b*). Its chromosomes are therefore not qualitatively differentiated (*v*. Ch. IX).

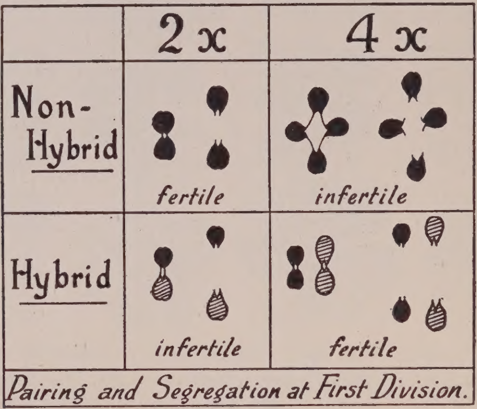


FIG. 55.—Diagram showing the basis of the inverse correlation of fertility of diploid and tetraploid. The fertile diploid gives a tetraploid with quadrivalents having inherently irregular division. The fertile tetraploid is derived from a diploid having segregation of dissimilar chromosomes.

An apparent exception to the fertility rule is provided by Hollingshead's tetraploid *Crepis* hybrid, which lacks both vigour and fertility. The explanation lies in its origin being exceptional in two respects: first, it is derived from a *C. capillaris* strain with irregular meiosis and defective fertility (*v.* Ch. XIII); secondly, it is derived from segregation in a triploid, unlike any of the other examples. It therefore probably has chromosomes which have suffered crossing-over with their homologues of the other species, and it is therefore not a strictly balanced type (*v.* Ch. IX).

2. POLYPLOID SPECIES

In about half the species of the angiosperms the gametic chromosome number is probably a multiple of that found in some related species, the chromosomes being themselves comparable in the related forms. From this alone it is clear that they owe their origin to polyploidy, tetraploids being derived from crosses between diploids and diploids, hexaploids from crosses between tetraploids and diploids, and so on. They may therefore be expected to resemble the polyploids produced in experiment.

Winge (1917), in a remarkable survey of these conditions, first suggested that they were likely to be of the type derived from hybridisation (allopolyploids). He considered that the need for a partner with which a chromosome could pair would stimulate doubling in hybrids. This teleological argument led to a sound general conclusion, although the argument itself is only admissible as a figure of speech. Somatic doubling probably occurs no more freely in haploids (in which the chromosomes have no conceivable partner) and in hybrids (in which they have no effective partners) than in homozygous diploids; it is more frequently *noticed* in haploids and hybrids because of the striking change it produces in them. Gametic doubling or failure of reduction does occur more freely in haploids and hybrids, but for the demonstrable reason that meiosis has proved unworkable—and not in anticipation of its doing so (Ch. XIII).

The observations of the relative fertility of auto- and allotetraploids provide sufficient reason for supposing that polyploid species will be of the hybrid kind where they depend on their sexual fertility for their reproduction. The evidence of the relationship of the constituent gametic sets of polyploids (*i.e.*, of the extent to which they are allo- or auto-polyploid) is provided by a series of observations which, owing to their importance for the theory of chromosome pairing, may be conveniently considered in relation to "differential affinity."

3. DIFFERENTIAL AFFINITY: AUTOSYNDESIS

In the diploid *Primula kewensis* the nine chromosomes of *P. verticillata* pair with the nine chromosomes of *P. floribunda*, their presumed homologues. In the tetraploid, however, each chromosome pairs with its identical mate, *floribunda* with *floribunda* and *verticillata* with *verticillata.* Only exceptionally one, two or three quadrivalents are formed through all four homologues associating. The explanation of this difference lies in the method of pairing amongst the similar threads at zygotene and of chiasma formation in the paired threads at diplotene, described in polyploids. If *floribunda* and *verticillata* chromosomes can only pair in half their length at pachytene this will probably suffice to ensure regular metaphase pairing by the formation of one chiasma in the diploid hybrid. In the tetraploid their chance of forming a chiasma would be reduced to two-thirds *if the similar parts continued to pair at random.* But from what we know of the structural differences between species (Chs. V and VI) we cannot assume that the differences in undefined hybrids are so simple as here suggested. Probably such portions of the corresponding chromosomes as can pair are distributed in several segments. There will then be several differences of linear sequence (or changes of homology) in the dissimilar chromosomes. Since the chromosomes in polyploids behave at zygotene as though they consisted of a small number of "pairing blocks" each of these changes of homology will prevent pairing in the block affected, while pairing between identical chromosomes will proceed unobstructed. Thus the existence of limited numbers of effective pairing blocks means that similar parts of dissimilar chromosomes, if they are short, do *not* pair at random in a polyploid; hence the differential affinity of dissimilar chromosomes in the presence and in the absence of identical partners.

An analogous observation has been made on a triploid hybrid containing two sets of *Crepis capillaris* and one of *Crepis tectorum* (Hollingshead, 1930 *b*). The *tectorum* chromosomes are regularly left unpaired, although they pair with the *capillaris* chromosomes in the diploid hybrid. Similarly the two Y chromosomes of *Rumex Acetosa* regularly pair with the corresponding parts of the X chromosome in the diploid, but in the triploid which contains $X X Y_1 Y_2$ they are left unpaired (Ono, 1928). The two X's are completely identical and pair to the exclusion of the Y's, which may be inferred from this to be identical with them only in small segments (Ch. XIV). Most striking examples of differential affinity are shown by the pairing of chromosomes in the haploid progeny of true diploids which have perfectly regular pairing. This will be described in another connection (Ch. IX).

Differential affinity is characteristic of the behaviour of homologous chromosomes of different sets in allopolyploid species, as compared with that in their "haploid," "triploid," and hybrid derivatives. In these derivatives, chromosomes derived from the same parental gamete pair with one another, although such pairing rarely occurs in the normal "homozygous" polyploid species, where each has an identical mate. In these circumstances the change in conditions seen in the doubling of the diploid *Primula kewensis* is reversed, and it is possible to understand the relationship that the natural polyploid has to the product of experiment such as *Primula kewensis.*

This "internal pairing" is known as *autosyndesis* and is opposed to *allosyndesis*, the pairing of homologous chromosomes derived from opposite parents (Ljungdahl, 1924). Both consist in the pairing of dissimilar chromosomes, and neither occurs in a true-breeding plant where identical chromosomes pair. The distinction between the two is merely relative to the immediate parents, but the occurrence of autosyndesis is significant in an allopolyploid's derivatives because it means that chromosomes pair in the absence of identical mates, although they rarely or never pair in the presence of such mates.

Autosyndesis occurs in the offspring of allopolyploids under the following conditions :—

1. *In the normal polyploid species as an exceptional occurrence.* Thus quadrivalents are occasionally found in the tetraploid *Primula kewensis* and in many allotetraploid species. In the hexaploids

Triticum vulgare and *Avena sativa* quadrivalents are found (Huskins, 1927, 1928). In all these instances aberrant offspring appear which evidently result from the segregation of dissimilar chromosomes (*i.e.*, through exceptional autosyndesis), since they have in a more marked degree the characters of one of the parental species (in *Primula kewensis*) or of a related species (in *Triticum* and *Avena*).

2. *In the " haploid " derived parthenogenetically from a polyploid.* Thus if *Solanum nigrum* (*6x*) consists of six sets, *AABBCC*, its " haploid " has the constitution *ABC*, and is relative to its basic number a triploid (*3x*). Pairing takes place between chromosomes of the different sets. From 5 to 12 bivalents and in the embryo-sac mother-cell even some trivalents are formed. The maximum association therefore corresponds with that found in the classical triploid *Drosera* hybrid (Jørgensen, 1928). Haploids derived from other polyploids have shown less autosyndesis, as follows :—

Triticum compactum ($6x = 42$), $0 - 3^{II}$. Gaines and Aase, 1926.
Nicotiana Tabacum ($4x = 48$), $0 - 3^{II}$. Chipman and Goodspeed, 1927.
Digitalis mertonensis ($16x = 112$), $5 - 12^{II}$. Buxton and D., 1932.

In these species the chromosomes are so far different that they pair very little even in the absence of competition. The species are approaching the condition of simple diploids. The variation found in pairing in all these " haploids " is characteristic of that of the diploid, triploid and other hybrids with which they correspond, and not unexpected (*cf.* Chipman and Goodspeed). In *Digitalis* the process of doubling by which the new species arose from a diploid hybrid has been reversed in the origin of the haploid form from it by parthenogenesis.

3. *In "triploids" that have arisen through the functioning of an unreduced gamete.* These have each of the dissimilar sets of chromosomes reproduced identically three times. Thus a tetraploid *AABB* gives a triploid *AAABBB*. Since only two chromosomes can pair at any one point at pachytene, the third set of *A* is left out of combination, and is therefore (at any one point) in the same

relationship to the corresponding but dissimilar set of *B* as it would be in a " haploid " *AB*. But at other points such third-chromosomes will be free to pair with their identical homologues, so that sexivalents will occasionally be formed as well as bivalents derived from autosyndesis within the third complement. Such is the condition in " triploid " *Pyrus Malus* (Nebel, 1929 ; D. and Moffett, 1930), the diploid form of which is a secondary polyploid (Ch. VIII). Seventeen bivalents are formed in the diploid ; quadrivalents are rare. But in the " triploid " more than seventeen bivalents are usually formed and frequently associations of six, *i.e.*, the third set pair among themselves (Fig. 56).

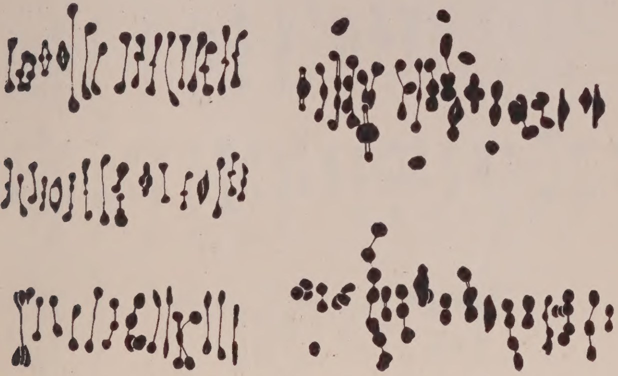


FIG. 56.—First metaphase in pollen mother-cells of *Pyrus* ($x = 17$). Left, diploid forms showing one or two exceptional quadrivalents. Right, triploids : above, 2^{I}, 5^{II}, 7^{III}, 1^{IV}, 1^{VI}, 1^{VII} ; below, 5^{I}, 10^{II}, 6^{III}, 2^{IV}. × 2500. (From D. and Moffett, 1930.)

4. *In hybrids of hexaploids, octoploïds and higher polyploids with diploids.* Two, three or more sets of the polyploid are naturally left without a partner, as they are in a haploid and triploid. They are frequently found to pair by autosyndesis. The diploid-hexaploid hybrid not only has the chromosome number of a tetraploid but also behaves like one in pairing. In one such case (*Prunus*) quadrivalents are frequently found in the hybrid, so that pairing is taking place between all three sets of the polyploid parent (Fig. 57). In

other cases (*Crepis* and *Papaver*) the hybrid can again be crossed with a diploid species and again yield a hybrid with complete pairing, thus :—

$$10x \times 2x = 6x\ (3x^{\text{II}}),\ 6x \times 2x = 4x\ (2x^{\text{II}}).$$

Here also pairing is occurring between all the sets of the polyploid.

5. *In hybrids between two tetraploid species.* Most of the chromosomes may fail to pair altogether, but some quadrivalents are found. Higher configurations often occur in the hybrid than in its polyploid parent, although very little pairing occurs at all (Kihara and Nishiyama, 1930 ; *v.* Fig. 58 ; Kattermann, 1931). This condition is found in hybrids between two tetraploids (*Triticum-Ægilops*, Kihara, 1929) and in *Viola* hybrids (*e.g.*, *V. nana* and *V. lutea*, J. Clausen, 1931 *c*). The formation of multivalents makes it possible to prove the occurrence of autosyndesis in a hybrid between two tetraploids. Thus in the cross *Ægilops cylindrica* ($4x = 28$) by *Æ. triuncialis* ($4x = 28$) a trivalent was sometimes found together with 6 to 11 bivalents (Kagawa, 1931). The trivalent could only arise through pairing of chromosomes derived from the same

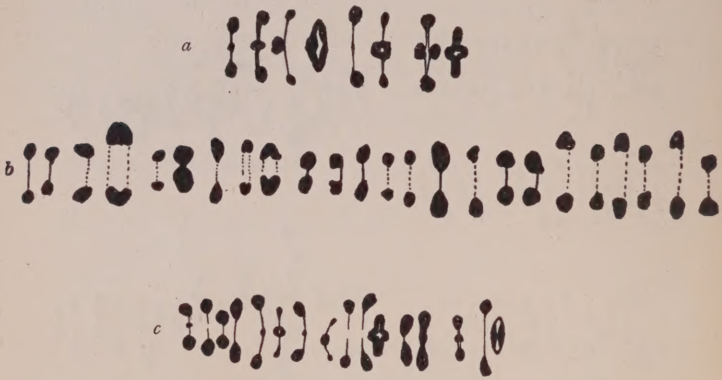


FIG. 57.—Side views of the pairing chromosomes at first metaphase : *a*, in *Prunus cerasifera*, $n = 8$; *b*, in *P. domestica*, $n = 24$; *c*, in the hybrid, *P. domestica* × *P. cerasifera*, $n = 16$. × 3000. (*b*, from Mather, unpublished ; *c*, from D., 1930 *a*.)

gamete, if not with one another at least with the same chromosome derived from the other gamete. Thus autosyndesis occurs in the hybrids when it does not occur in their parents.

The simplest case of this is the formation of occasional quadrivalents by the hybrid between the tetraploid species *Triticum turgidum* and *T. durum* which themselves have simple pairing (D., 1931 *d*). This indicates that among the pairs also in this hybrid there may be some consisting of chromosomes derived from

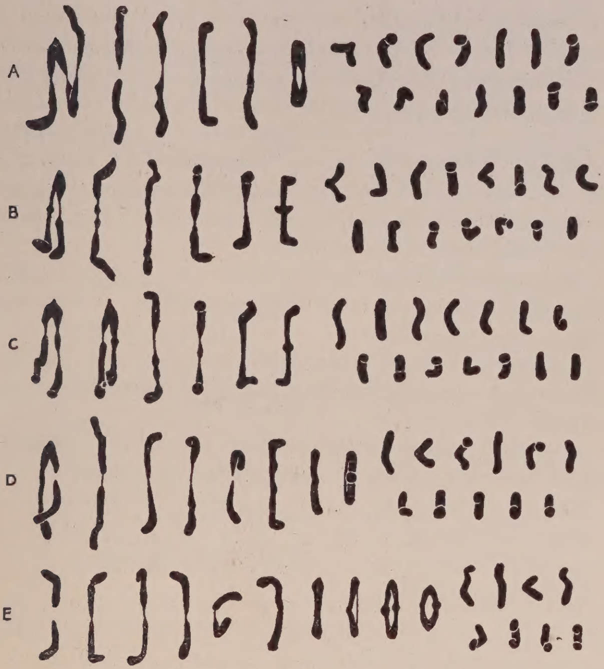


FIG. 58.—First metaphase in the tetraploid hybrid ($4x = 28$) of *Triticum Spelta* ($6x$) × *T. ægilopoides* ($2x$) showing the variation in pairing from nucleus to nucleus. A, $1^{IV} + 5^{II} + 14^{I}$; B, $1^{III} + 5^{II} + 15^{I}$; C, $2^{III} + 4^{II} + 14^{I}$; D, $1^{III} + 7^{II} + 11^{I}$; E, $10^{II} + 8^{I}$. All chiasmata are terminal or subterminal. × 1400. (From Kihara and Nishiyama, 1930. *Cf.* Fig. 49.)

the same parent. Thus segregation of the characters carried by the ultimate diploid parents may be expected. This " secondary segregation " has been found in the progeny of similar crosses in *Triticum* (*cf.* D., 1928).

Finally there are hybrids (especially triploids) where the relationships of the pairing chromosomes cannot be stated with certainty. In the *Drosera* hybrid (Rosenberg, 1909) it was assumed that the unpaired chromosomes were those of the tetraploid parent, but they may (at least in part) be those of the diploid as a result of autosyndesis. Similarly in the *Beta* hybrid it is not possible to know the provenance of the pairing chromosomes (*cf.* Table 28 D).

The different kinds of autosyndesis may be summarised, giving the same chromosome type the same capital letter, but a different number when dissimilar, as follows :—

1. Allotetraploid species ($4x$, $2x$ pairs) : A_1–A_1, A_2–A_2, B_1–B_1, B_2–B_2, etc., shows exceptional autosyndesis, A_1–A_1–A_2–A_2, B_1–B_1, B_2–B_2, etc.

2. " Haploid " derived from it by parthenogenesis, or diploid hybrid giving rise to it by doubling ($2x$, x pairs) shows autosyndesis : A_1–A_2, B_1–B_2, etc.

3. " Triploid " derived from tetraploid by fusion of reduced and unreduced gametes ($6x$) shows autosyndesis :—

A_1–A_1, A_1–A_2, A_2–A_2, B_1–B_1, etc.
or A_1–A_1–A_1–A_2, A_2–A_2, B_1–B_1, etc.
or A_1–A_1–A_1–A_2–A_2–A_2, B_1–B_1, etc.

4. Hybrid of a hexaploid species ($6x$, $3x$ pairs) : A_1–A_1, A_2–A_2, A_3–A_3, B_1–B_1, etc., and a diploid species ($2x$, x pairs), A_4–A_4, B_4–B_4, etc. ($4x$) shows autosyndesis :—

A_1–A_2, A_3–A_4, B_1–B_2, etc.
or A_1–A_2–A_3–A_4, etc.

5. Hybrid with another tetraploid species (A_3–A_3, A_4–A_4, B_3–B_3, etc.) ($4x$) shows autosyndesis except in the last example :—

A_1–A_2, A_3–A_4, B_1–B_2, B_3–B_4
or A_1–A_2–A_3–A_4, etc.
or A_1, A_2, A_3–A_4, etc.
or A_1–A_3, A_2–A_4, B_1–B_3, etc.

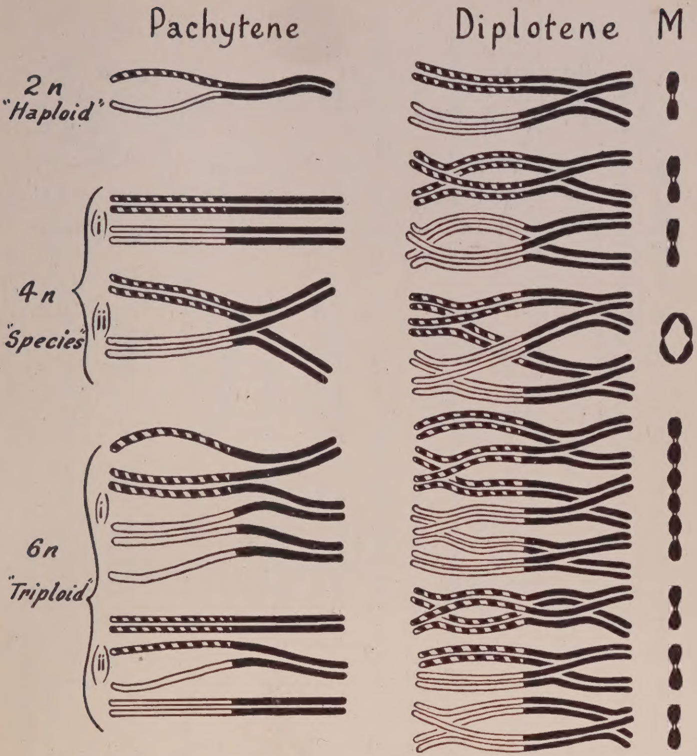


FIG. 59.—Diagram showing the method of pairing in an allotetraploid species and in the "haploid" and "triploid" derived from it on the assumption that the dissimilar chromosomes are similar and capable of pairing, in the absence of competition, in half their length. M, metaphase; black, similar segments; white and hatched, dissimilar ones. *Note:* pairing of dissimilar chromosomes is inevitable in "haploid" and "triploid" but only possible in the face of competition in the species, whence differential affinity. (i) and (ii) are alternative possibilities with and without autosyndesis. For *n* read *x*.

The conditions determining these results, on the assumptions (i) that the differences which reduce pairing at pachytene are structural; (ii) that pairing is limited amongst identical segments

TABLE 28

Pairing of Chromosomes in Hybrids and Hybrid Derivatives of Polyploid Species

A. HYBRIDS BETWEEN HIGH AND LOW POLYPLOIDS SHOWING POTENTIALLY COMPLETE AUTOSYNDESIS

Authority.	Genus.	Basic Number.	Species Crossed.	Hybrid.	Pairing.
1. Haase-Bessel (1921) (*cf.* Buxton and Newton, 1928).	*Digitalis.*	7	*lutea* (28^{II}) × *micrantha* (14^{II})	$6x$	21^{II}
2. Collins and Mann (1923).	*Crepis*	4 and 5	*setosa* (4^{II}) × *biennis* (20^{II})	—	10^{II} (*b*) + 4^{I} (*s*)
3. Collins, Hollingshead and Avery (1929).	"	"	F_1 × *biennis*	$6x$	15^{II} (*b*)
4. " " "	"	"	F_2 (" *C. artificialis*," 10^{II} (*b*) + 2^{II} (*s*)) × *setosa*.	—	5^{II} (*b*) + 2^{II} (*s*) + 2^{I} (*s*)
5. Ljungdahl (1924)	*Papaver.*	7	*nudicaule* (7) × *radicatum* (35)	$6x$	21^{II}
6. " "	"	7	*nudicaule* var. *striatocarpum* (35^{II}) × *nudicaule* (7^{II}).	$6x$	21^{II}
7. " "	"	7	F_1 × *nudicaule*	$4x$	14^{II}
8. Helms and Jørgensen (1925).	*Betula*	7	*verrucosa* (14^{II}) × *pubescens* (28^{II}).	$6x$	21^{II}
9. D. (1928, 1930 *a*)	*Prunus*	8	*domestica* (24^{II}) × *cerasifera* (8^{II})	$4x$	16^{II}
10. Crane and D. (1928)	*Rubus*	7	*rusticanus* (7^{II}) × *thyrsiger* (14^{II})	$4x$	14^{II} *
11. Tahara and Shimotomai (1931).	*Chrysanthemum*	9	*marginatum* (45^{II}) × *lavandulæfolium* (9^{II})	$8x$	36^{II} †
12. —	—	—	*Decaisneanum* (36^{II}) × *indicum* (18^{II})	$6x$	27^{II}
13. —	—	—	*marginatum* (45^{II}) × *morifolium* (27^{II})	$8x$	36^{II}
14. Andersson and Gairdner (1931).	*Dianthus*	15	*plumarius* (45^{II}) × *Knappii* (15^{II})	$4x$	*ca.* 30^{II} (F_1 and F_2).
15. Mangelsdorf and Reeves (1931).	*Tripsacum* *Zea*	18 10	*Z. Mays* (10^{II}) × *T. dactyloides* (36^{II})	—	18^{II} + 10^{I}

* Occasional quadrivalents and tetraploid segregation.

† Suggested that each parental gamete had nine extra chromosomes, but more probably the diploid parent produced a triploid gamete.

B. Hybrids showing Partial and Variable Autosyndesis

1. Shimotomai (1931)	*Chrysanthemum*	9	*marginatum* (45^{II}) × *indicum* (18^{II})	$7x$	$18^{II} + 27^{I}$ *
2. J. Clausen (1931 *c*)	*Viola*	(?)	*lutea* (24) × *elegantula* (10)	—	$14-15^{II}$, $6-4^{I}$
3. ,, ,,	,,	,,	*tricolor alba* (13) × *nana* (24)	—	$16-18^{II}$, $5-1^{I}$
4. ,, ,,	,,	,,	*tricolor alba* (13) × *rothomagensis* (17)	—	ca. 1^{IV}, $2-3^{III}$, $3-6^{I}$, and bivalents.
5. Yarnell (1931 *a*)	*Fragaria*	7	*vesca* (7^{II}) × *glauca* (28^{II})	5	$14^{II} + 7^{I}$ (and multivalents, *v.* Ch. V).
6. ,, ,,	,,	7	*vesca* (7^{II}) × *virginiana* (28^{II})		

* Occasional quadrivalents.

C. Potentially Complete Absence of Autosyndesis

1. Melburn and Thompson (1927).	*Triticum*	7	*spelta* (21) × *monococcum* (7)	$4x$	$0-5^{II}$
2. Kihara and Nishiyama (1930).	,,	7	*spelta* (21) × *ægilopoides* (7)	$4x$	$6-10^{II}$ or ^{III}
3. ,, ,, ,,	,,	7	*durum* (14) × *vulgare* (21)	$5x$	$13-14^{II}$ or ^{III}
4. Kihara (1924), Thompson (1926 *a*)	*Triticum* and *Secale.*		*T. vulgare* (21) × *S. cereale* (7)	$4x$	$0-3^{II}$
5. Ichijima (1930)	*Fragaria*	7	*bracteata* (7) × *virginiana* (28)	$5x$	$7^{II} + 21^{I}$
6. ,, ,,	,,	7	*californica* (7) × *chiloensis* (28)	$5x$	
7. ,, ,,	,,	7	*alba rosea* (7) × *chiloensis* (28)	$5x$	
8. Morinaga (1929)	*Brassica*	?9	*cernua* (18) × *Napellus* (19)	$4x+1$	$10^{II} + 17^{I}$
9. Bleier, 1928	*Beta*	9	*vulgaris* (9^{II}) × *trigyna* (27^{II})	$4x$	$9^{II} + 18^{I}$
10. Haase-Bessel (1916) (*cf.* Buxton and Newton).	*Digitalis.*	7	*purpurea* (28^{II}) × *lutea* (56^{II})	$12x$	0^{II} (*cf.* Table A1)
11. Haase-Bessel (1922)	,,		*lanata* (28^{II}) × *lutea* (56^{II})	$12x$	0^{II} (*cf.* Table A1)
12. J. Clausen (1931 *c*)	*Viola* '	7?	*Kitaibeliana* (7^{II}) × *arvensis* (17^{II})		$2-6^{II}$
13. ,, ,,	,,	,,	*nana* (24^{II}) × *Kitaibeliana* (7^{II})		$5-6^{II}$
14. ,, ,,	,,	,,	*Kitaibeliana* (i) (7^{II}) × *Kitaibeliana* (ii) (18^{II}).		ca. 6^{II}

D. Pairing in Triploid Hybrids (*cf.* Table 26)

1. *AAB* type (crosses between diploids with doubling of one set) *

Authority.	Genus.	Basic Number.	Species Crossed.	Hybrid.	Pairing.
1. Håkansson (1929 *b*) .	*Salix* . .	19	*viminalis* (19) × *caprea* (19) . .	$\left(vs + \frac{vs}{2}\right)$	$16-19^{III}$
2. Müntzing (1930 *b*) .	*Galeopsis* .	8	*pubescens* (8) × *speciosa* (8) . .	(*pss*)	$8^{II} + 8^{I}$
3. Poole (1931) . .	*Crepis* . .	5	*rubra* (5) × *fœtida* (5) . . .	$\left(rf + \frac{rf}{2}\right)$	—
4. Hollingshead (1930 *b*)	,, . .	—	*capillaris* (3) × *tectorum* (4) . .	(*cct*)	$3^{II} + 4^{I}$ rarely 1^{III}
5. Karpechenko (1927, *a* and *b*).	*Raphanus* and *Brassica*.	9	[*R. sativus* (9) × *B. oleracea* (9)] × *R. sativus*.	(*rrb*)	$9^{II} + 9^{I}$
6. Pariser (1927) . .	*Saturnia* .	—	*pavonia* (29) × [*pyri* (3) × *pavonia* (29)].	(*pv. pv. pr*)	—
7. Federley (1930) .	*Pygæra* . .	—	*pigra* (23) × [*pigra* × *curtula* (29)] .	(*ppc*)	$23^{II} + 29^{I}$

* The letters in brackets show the constitution of the triploid in regard to the sets of its two parents. The third set of the *Salix* and *Crepis* hybrids is mixed.

D. TRIPLOID HYBRIDS (continued)

2. *ABC* type (crosses between diploid and allotetraploid species). *Cf.* also structural hybrids.

Authority.	Genus.	Basic Number.	Species Crossed.	Pairing.
1. Rosenberg (1909)	*Drosera*	10	*longifolia* (10) × *rotundifolia* (20)	$10^{II} + 10^{I}$
2. „ (1917)	*Hieracium*	9	*auricula* (9) × *aurantiacum* (18)	$9^{II} + 9^{I}$
3. Ljungdahl (1922)	*Papaver*	7	*atlanticum* (7) × *dubium* (14)	$0^{II} + 21^{I}$
4. Goodspeed, Clausen and Chipman (1926); 5, 6. Goodspeed and Clausen (1927 *b*).	*Nicotiana*	12	*sylvestris* (12) × *Tabacum* (24) *tomentosa* (12) × *Tabacum* (24) *paniculata* (12) × *rustica* (24)	$12^{II} + 12^{I}$
7. Goodspeed and Clausen (1927).	„	12	*Bigelovii* (24) × *glutinosa* (12)	$0_{1}^{I} + 36^{I}$
8. Brieger (1928)	„	12	*Tabacum* (24) × *Rusbyi* (12)	$12^{II} + 12^{I}$
9. Sax (1922), Thompson (1926 *b*)	*Triticum*	7	*monococcum* (7) × *turgidum* (14)	$7^{II} + 7^{I}$
10. Kihara (1924)	„	7	*dicoccum* (14) × *monococcum* (7)	$4-7^{II} + 13-7^{I}$
11. Kihara and Nishiyama (1930).	„	7	*ægilopoides* (7) × *diccocum* (14)	$0-3^{III}+4-7^{II}+6-7^{I}$
12. Berg (1931)	*Ægilops* and *Secale*.	7	*A. triuncialis* (14) × *S. cereale* (7)	$5-7^{II} + 11-7^{I}$
13. Jørgensen (1927)	*Lamium*.	9	*dissectum* (18) × *amplexicaule* (9).	$9^{II} + 9^{I}$
14. Fukushima (1929)	*Brassica* and *Raphanus*.	9	*B. cernua* (18) *and B. juncea* (18) × *R. sativus* (9).	$0^{II} + 27^{I}$
15. Wakakuwa (1931)	*Celosia*	18	*argentea* (36) × *cristata* (18)	$18^{II} + 18^{I}$

D. (continued)

3. Of Unknown Origin and Composition (Species, etc.).

Authority.	Genus.	Basic Number.	Species.	Somatic Number.	Pairing.
1. Rosenberg (1917, 1927)	*Hieracium*	9	*boreale*, *lævigatum*, *pseudoillyricum*, *umbellatum*, etc.	$3x=27$	few pairs
2. de Vilmorin (1929)	*Solanum*	12	*Commersonii*	$3x=36$	—
3. Rybin (1929 *b*)					
4. ,, ,,	,,	12	*coyacanum*	$3x=36$	—
5. ,, ,,	,,	12	*medians*		
6. ,, ,,	,,	12	" *tuberosum* " vars.		
7. D. (1928)	*Prunus*	8	*avium nana* (? *avium* × *cerasus*)	$3x=24$	$1\text{–}8^{III}$
8. Moffett (1931)	*Pyrus*	17	*minima* (?*ABC* type)	$3x=51$	$0\text{–}4^{III}$, $17\text{–}14^{II}$, $13\text{–}16^{I}$
9. Peto (1932)	*Festuca*	7	*loliacea*	$3x=21$	—

E. AUTOSYNDESIS IN " TRIPLOIDS " DERIVED FROM ALLOPOLYPLOIDS

Authority.	Species.	Somatic Number.	Basic Number.	Pairing.
1. Collins *et alii* (1929)	*Crepis artificialis*, mutant	$2n=36$	$x=5$	$17^{II} + 2^{I}$
2. Nebel (1929), D. and Moffett (1930).	*Pyrus Malus*, vars.	$2n=51$	$x=7$	less than 17^{I}.
3. Moffett (1931)	*Cratægus monogyna*, var.	$2n=51$	$x=7$	
4. Buxton and Newton (1928)	*Digitalis mertonensis* × *D. ambigua*	$2n=84$	$x=7$	more than 28^{II}

F. PAIRING IN MULTI-SPECIFIC HYBRIDS

1. Pairing of chromosomes in the characteristic allopolyploid *Raphanus-Brassica* and its derivatives (trispecific hybrids). Karpechenko, 1927, *a* and *b*, 1929

Raphanus sativus . . .	(Rs)	$n = 9 = x$ ...	Rs.Bo	$(2x = 18)$ ...	0^{II} (18^{I})
R. raphanistrum . . .	(Rr)	$n = 9 = x$ ...	Rs.Rs.Bo.Bo	$(4x = 36)$ ...	18^{II}
Brassica oleracea . . .	(Bo)	$n = 9 = x$ ...	Rs.Rs.Bo	$(3x = 27)$ ...	9^{II} (9^{I})
B. campestris . . .	(Bcp)	$n = 10 = x$ ...	Rs.Bo.Rr	$(3x = 27)$ ...	9^{II} (9^{I})
B. carinata . . .	(Bcr)	$n = 17 = 2x$? ...	Rs.Bo.Bcp.	$(4x = 28)$ ...	$5\text{–}6^{II}$ $(15\text{–}17^{I})$
			Rs.Bo.Bcr.	$(4x = 35)$ ...	$9\text{–}17^{II}$ $(17\text{–}1^{I})$

2. Pairing in a hybrid of two new hybrid polyploids (quadrispecific hybrids) *v.* Berg, 1931 *b*.

Ægilotricum, $7x$ (= *Ægilops ovata*, 14, + *Triticum durum*, 14) × *Triticum turgidovillosum*, $6x$ (= *T. turgidum*, 14 + *T. villosum*, 7).

$$7x = 49\,;\ 12\text{–}14^{II},\ 25\text{–}21^{I}.$$

in a polyploid when they are not in the same sequence throughout the chromosomes ; and (iii) that pairing at metaphase is determined by the formation of chiasmata in the pachytene thread proportionate in number to the length paired, are illustrated in the diagram (Fig. 59).

On such assumptions the corresponding chromosomes derived from opposite species might be represented as a series of gene-blocks or segments *abcdefg* and *adfgbe*. When two such chromosomes are free to pair together they may do so with great regularity, but in the presence of identical mates (in the normal allotetraploid of the constitution *abcdefg*, *abcdefg* and *adfgbe*, *adfgbe*) they will rarely if ever pair, on account of *d*, *b* and *e* being in a different sequence in the chromosomes of the two species. These observations of differential affinity are therefore in accordance with the theories of structural hybridity and chromosome pairing arrived at on other grounds.

All the different conditions of autosyndesis have not been obtained in one and the same polyploid, but it is possible to associate groups of species according to their behaviour in autosyndesis, since, whatever the conditions, this pairing indicates a certain degree of similarity between the pairing chromosomes. The classification is arbitrary, the more so since the observations on which it is founded have generally been defective in two ways : (i) they have taken little account of variations in the frequency of pairing from cell to cell ; (ii) they have overlooked the formation of multivalents. Comparison, however, shows a close analogy between the results of the *synthesis* of new species by doubling and *analysis* of old species by parthenogenesis and hybridisation. They show in allopolyploid species a range of variation from the *Primula kewensis* type to the *Raphanus-Brassica* type.

4. CLASSIFICATION OF POLYPLOID SPECIES

Observations of differential affinity show that every gradation occurs in the relationship of the homologous chromosomes in the gametic complement of polyploids. As a rule these chromosomes can be considered in sets, for the same conditions have operated to secure the degree of differentiation found between pairs of homologues in any two. The different kinds of polyploid species may therefore be classified, arbitrarily but conveniently, in three groups.

The first class includes those in which autosyndesis never occurs in haploids, triploids or hybrids, or *a fortiori* in the normal species. This extreme of differentiation, found in *Nicotiana Tabacum* and in *Triticum compactum*, is analogous to that in the *Raphanus-Brassica* tetraploid. It is probably found most generally in old established seed-producing annual species.

The second class consists of those species with imperfect differentiation. The pairing observed in *Bromus erectus* may serve as a type of behaviour in this group. Table 30 shows pairing in one plant; in others a sexivalent and octavalent were found. The occurrence of univalents in 9 per cent. of the cells is probably due to mechanical interference with pairing at zygotene as in tetraploid *Primula sinensis*, and is therefore a symptom of autopolyploidy.

Following is a list of similar species whose pairing is normally and "legitimately," as we may say, that of diploids, but in which multivalents are occasionally and illegitimately formed. In these, more or less autosyndesis is found, or is to be expected, in haploids and hybrids.

TABLE 29

Polyploid Species of an Intermediate Type

Rumex Acetosella (6*x*, 42)	Kihara, 1927; Ono, 1930.
Triticum vulgare (6*x*, 42)	Winge, 1924; Huskins, 1928.
Avena sativa (6*x*, 42)	Huskins, 1927.
Bromus erectus eu-erectus (8*x*, 56)	Kattermann, 1931.
Rubus thyrsiger (4*x*, 28)	Crane and D., 1927.
Prunus domestica (6*x*, 48)	D., 1930 *a*.
P. spinosa (4*x*, 32)	
P. laurocerasus (22*x*, 176)	Meurman, 1929 *a*.
Pyrus Malus (4–6*x*, 34)	D. and Moffett, 1930 (*v*. p. 224).
Cardamine pratensis (4*x*, 30)	Lawrence, 1931 *b*.
Lythrum Salicaria (6*x*, 30)	Shinke, 1929.
Tulipa stellata (4*x*, 48)	D. and Janaki-Ammal, 1932.

TABLE 30

Pairing in *Bromus erectus* var. *eu-erectus* ($2n = 56 = 8x$, Kattermann, 1931)

Type of pairing .	28^{II}	2^{I}	$1^{III} + 1^{I}$	2^{III}	1^{IV}	2^{IV}	Not Determined.	Total.
Number of cells .	1,006	99	5	2	11	2	26	1,151

The third class consists of species in which there is no clear differentiation of the corresponding chromosome sets. They may even, in some forms, be considered identical. They occur as triploids (the result of doubling in one parental gamete) tetraploids (the result of doubling in both parental gametes or somatically) and pentaploids (the result of doubling on two occasions). The tetraploids are of somewhat reduced fertility, while the triploids and pentaploids are almost entirely sterile. In this they resemble

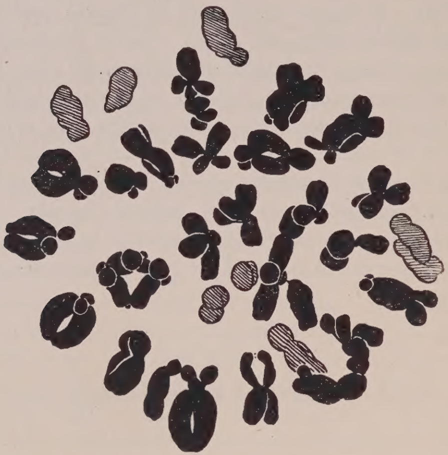


FIG. 60.—First metaphase in *Tulipa Clusiana* ($5x = 60$) showing 8 univalents (hatched), 15 bivalents, 3 trivalents, 2 quadrivalents and one quinquevalent. × 4000. (From Newton and D., 1929.)

polyploid species that are interchange heterozygotes, and must depend entirely on vegetative propagation for their continued existence.

With these species, polyploids having the behaviour of simple structural heterozygotes may conveniently be considered, for the reasons given earlier (Ch. V).

TABLE 31

Autopolyploid Species and Mutants
(basic numbers in brackets)

A. TRIPLOIDS (*cf.* Table 20 (*b*))

1. Wild Species (asexually reproduced) :—

Lilium tigrinum (12)	Takenaka and Nagamatsu, 1930 (*v.* Table 15).
Tulipa præcox (12)	D., unpublished.
Tulipa saxatilis (12)	D., unpublished.
Hydrilla verticillata (8)	Sinoto, 1929.
Alnus cordata, etc. (7)	Jaretsky, 1930.
Lycoris radiata (11)	Nishiyama, 1928.
L. squamigera (9)	Takenaka, 1930.
Trichoniscus provisorius (8)	Vandel, 1928 (*v.* Ch. XV).

2. Mutants of Species (occasional seedlings from unreduced gametes) :—

C. capillaris (3)	Navashin, 1926.
Rumex Acetosa (8) (discovered through examination of intersexes).	Ono, 1928, 1930; Ono and Shimitomai, 1928.
Ranunculus acris (6) (probably 3*x*, gynodimorphic).	Sorokin, 1927 *a*.
Zea Mays (10)	Randolph and McClintock, 1926; McClintock, 1929 (7–10^{III}).
Nicotiana alata (9)	Ruttle, 1928; Avery, 1929 (monosomic diploid selfed).
Drosophila melanogaster (4)	Bridges, 1921 *a*; Metz, 1926.

2A. Cultivated Forms (vegetatively propagated) :—

Hyacinthus orientalis (8)	De Mol, 1923; Belling, 1925, 1927; D., 1926, 1929 (highly fertile).
Tulipa Gesneriana vars. (12)	De Mol. 1925; Newton and D., 1929.
Canna spp. (9)	Belling, 1921, 1925 *d*.
Fritillaria pudica (13)	D., unpublished.
F. latifolia major (12)	D., unpublished.
Iris japonica (18)	Kazao, 1929.
I. florentina (16)	Kazao, 1929.
Narcissus poeticus var. (7)	Nagao, 1929.
Hemerocallis fulva (11)	Belling, 1925 *d*; Takenaka, 1929.
Morus spp. (14)	Osawa, 1921 (parthenocarpic).
Prunus Mume (8)	Okabe, 1927.
P. serrulata, etc. (8)	Okabe, 1927 (11 vars. $3x$; 30, $2x$).
Pyrus Malus vars. (17)	Rybin, 1927; D. and Moffett, 1930.
Cratægus monogyna var.	Moffett, 1931, *a* and *b*.
Primula Sieboldii (12)	Ono, 1927.

3. Experimental Hybrids ($2x \times 4x$) :—

Vicia Cracca (7)	Sveshnikova, 1929.
Solanum Lycopersicum (12)	M. M. Lesley, 1929 ($9\text{–}10^{\mathrm{III}}$).
Datura Stramonium (12)	Belling, 1927 (12^{III}).
Primula sinensis (12)	Dark, 1931 ($8\text{–}9^{\mathrm{III}}$).
Campanula persicifolia (8)	Gairdner and D., 1931 ($3\text{–}5^{\mathrm{III}}$).
Nicotiana Tabacum (24)	Goodspeed, 1930 (X-rayed).

B. TETRAPLOIDS (*cf.* Table 20 (*c*))

1. Wild Species :—

Avena elatior (7)	Kattermann, 1931.
Prunus Cerasus (certain forms) (8)	D., 1928.
Allium schœnoprasum var. *sibiricum* (8)	Levan, 1931.

2. Mutants of Species :—

Amblystegium serpens (11)	E. and E. Marchal, 1911, 1912.
Funaria hygrometrica (7)	*v.* Wettstein, 1924, 1928.
Primula sinensis (12)	*Cf.* D., 1931 *a*.
Datura Stramonium (12)	*Cf.* Blakeslee *et al.*, 1923.
Solanum Lycopersicum (12)	Jørgensen, 1928 ; Lesley, 1930 ; and Sansome, 1930.
S. nigrum (36)	Jørgensen, 1928.
Citrus Limonum, etc. (9)	Frost, 1925.
Crepis capillaris (3)	Navashin, 1926.
C. tectorum (4)	Navashin, 1926 (fertile).
Primula obconica (12)	Sansome and Philp, 1932.
P. malacoides (11)	Newton (*cf.* Tischler, 1931) ; Philp, unpublished ; Kattermann, unpublished.
Campanula persicifolia (8)	Gairdner, 1926 ; Gairdner and D., 1932.

C. PENTAPLOIDS

1. Wild Species :—

Tulipa Clusiana (12)	Newton and D., 1929 (Figs. 60—61).
Ochna serrulata (7)	Chiarugi and Francini, 1930.

2. Mutant of Species :—

Crepis tectorum (5)	Navashin, 1926 (Fig. 13).

D. OCTOPLOID

1. Wild Species :—

Crepis biennis (5)	Collins, Hollingshead and Avery, 1929.

The triploids form a majority of trivalents, the tetraploids a majority of quadrivalents. The higher configurations possible in the pentaploids necessarily make the kind of association more variable, but it is characteristically different from that in allopentaploids. Thus in pentaploid *Triticum* and *Nicotiana* (Kihara and Nishiyama, 1930 ; and Webber, 1930) four chromosome sets are associated as pairs, and the fifth is chiefly unpaired; trivalents are formed, even, in one hybrid to the number of twelve (Brieger, 1928; Table 26). Chromosome behaviour in the two pentaploid species *Ochna serrulata* and *Tulipa Clusiana* is entirely different. They both form a high proportion of multivalents (Fig. 60). A new mutant autopentaploid (such as that found by Navashin, 1926, in *Crepis capillaris*) has not yet been examined for comparison, but from what we know of the behaviour of non-hybrid triploids and tetraploids, these pentaploids must also be non-hybrid. It is, however, possible on cytological grounds that they consist of five sets equally (and not strongly) differentiated. Both species are sexually sterile, the one reproducing by apomixis (Ch. XV), and the other by bulbs. They are clonal species.

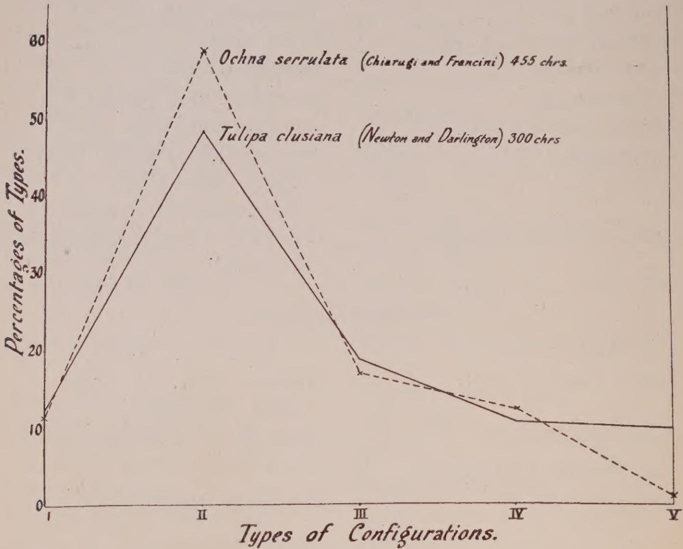


FIG. 61.—Graph showing the percentages of different types of configuration in two autopentaploid species at meiosis in the pollen mother-cells. The more frequent high configurations in *Tulipa Clusiana* are probably due to a higher chiasma frequency.

The last class of polyploids includes high multiples, which probably always have different degrees of relationship between different sets, for two reasons: the complexity of their origin and the lower effectiveness of balance in requiring constant allopolyploidy. The characteristic of these species is variability in the chromosome number, for the irregular segregation of the multivalents gives gametes with various numbers; owing to the high gametic number the unbalance of these is less serious than it would be in low polyploids, and they are not eliminated (*v*. Ch. IX).

Following is a list of species of this type with the numbers of somatic chromosomes found or inferred in each.

TABLE 32

Polyploid Species with Variable Numbers

Cochlearia anglica, 37–44, 49, 50	Crane and Gairdner, 1923.
Salix triandra, 38, 44	Blackburn and Harrison, 1924.
Prunus laurocerasus, *ca*. 176	Meurman, 1929.
Crepis biennis, 39–45	Hollingshead and Babcock, 1930.
C. ciliata, 40–42	
Viola canina, 40–47	J. Clausen, 1931 *b*.
V Battaudieri, 52–60	J. Clausen, 1931 *c*.

CHAPTER VIII

THE EVOLUTION OF POLYPLOIDS

Cell Size and Chromosome Number—In Experimental Polyploids—In Polyploid Species—Statistical Evidence of Polyploidy—New Polyploid Species—Somatic and Secondary Pairing—Secondary Polyploids.

1. THE DEVELOPMENT OF THE POLYPLOID SPECIES

(i) **Introduction.** The increase of chromosome number by which a polyploid arises has been reversed in experiment, first, by crossing an autopolyploid with its diploid relatives and selfing the triploid progeny, or back-crossing them to the diploid (as in *Solanum*, *Campanula*, *Primula sinensis*); or, secondly, by parthenogenesis, in which an autotetraploid gives its fertile diploid parent (as in *Campanula*, Gairdner and D., 1931), and an allotetraploid gives its sterile diploid parent (as in *Digitalis*, Buxton and D., 1931). Thus when the allopolyploid reverts to the diploid, sterility is produced, which can only be got rid of by another doubling of the chromosome number. Chromosome doubling in a hybrid must therefore be an irreversible process in nature. On these and other grounds it is to be supposed that polyploid species are often of great antiquity, and this suggests two problems: How is a polyploid species to be recognised as such? And how do polyploid species change after their origin? The second problem will be considered first.

(ii) **Variation in Cell Size.** External and developmental factors influence the size of the cell and of its nucleus, but, these factors being equal, the size might be expected to be proportionate to the number of chromosomes of which the nucleus is constituted when the number is simply doubled or halved. This condition is realised immediately after the formation of a new nucleus in the pollen. Diploid pollen grains have 1·25 times the linear dimensions and twice the bulk of haploid pollen grains (Belling on *Uvularia*, 1925; *Solanum*, Fig. 53). The same applies with certain restrictions to the cells of all parts of the organism, and is equally true of the polyploid derivatives of hybrids and pure forms, as shown by v. Wettstein (1924) with diploid, tetraploid and octoploid mosses, and by the other authors cited.

TABLE 33

Recent Comparative Measurements of Cells in Haploids, Diploids and Polyploids

Animals :—	
Drosophila melanogaster (*x*, 2*x*, 3*x*).	Bridges, 1925 *b*.
Artemia salina (2*x*, 4*x*, wild races).	Artom, 1928.
Trichoniscus provisorius (2*x*, 3*x*, wild races).	Vandel, 1927 *b*.
Plants :—	
Datura (*x*, 2*x*, 4*x*)	Blakeslee, 1922 ; Belling and Blakeslee, 1927.
Crepis (*x*, 2*x*)	Hollingshead, 1928.
Crepis capillaris (*x*, 2*x*, 3*x*, 4*x*).	Navashin, 1931 *b*.
Œnothera (*x*, 2*x*)	Emerson, 1929 ; Gates and Goodwin, 1931.
Raphanus-Brassica (2*x*, 3*x*, 4*x*, 6*x*).	Karpechenko, 1927, *a* and *b*.
Nicotiana digluta (2*x*, 4*x*)	Clausen and Goodspeed, 1925.
Funaria, etc. (2*x*, 4*x*, 8*x*)	v. Wettstein, 1924.
Uvularia (*x*, 2*x*)	Belling, 1925 (pollen grains).
Solanum (*x*, 2*x*)	Jørgensen, 1928 (pollen grains).
Tradescantia (*x*, *x* + 1, *x* + 2, etc.).	D., 1929 *c* (pollen grains).

While the proportion between size and chromosome number is fairly closely maintained so far as cells are concerned, intracellular structures such as chloroplasts may be increased in number instead of in size, and multicellular structures are developed in changed proportions. The vigour of the organism as a whole is usually reduced by reduction or multiplication of the chromosome number, and its size therefore does not change proportionally. A reduction in the number of cells in corresponding organs of the plant is found after doubling twice in *Funaria hygrometrica* (v. Wettstein, 1924), and after doubling only once in *Acrocladium cuspidatum*. The haploid is usually of a more immature, stripling growth than the diploid, while the tetraploid is of a stouter growth (Jørgensen, 1928; Davis and Kulkarni, 1930; Clausen and Mann, 1924). It should be noted that this applies to the fruits for different reasons. The development of many-seeded fruits is often proportional to their seed content, which is lower in haploids, triploids and non-hybrid tetraploids than in the corresponding diploids. Hence the fruits are smaller in these, and often of different shapes (Blakeslee and Belling, Jørgensen).

Organisms are therefore modified in general character by a change in their size, *i.e.*, by a change in volume-surface relations. The same chromosome complement, in fact, always has a qualitatively as well as a quantitatively different phenotypic expression when represented different numbers of times, and changes from the condition to which it is adapted, whether haploid, diploid or tetraploid, are more or less deleterious, just as are changes of balance. This principle is of importance in considering the origin of the special differentiation found in species where the male is haploid and the female diploid. In these the complement is adapted to both the haploid and the diploid conditions. The differentiation in phenotypic expression is then carried to an extreme. It applies even to cell-size. Exceptional diploid males in *Habrobracon* are no larger than the normal haploids (Torvik, 1931). Special genes or gene-combinations can therefore be selected to modify the ordinary relationship of the size of the organism to that of the nucleus when the chromosome number is altered, just as they are evidently selected to modify the sexual character of the organism (Ch. XVI). Simple doubling in species not specialised in this exceptional way is always accompanied by more or less gigantism. Where the polyploid form shows no increase in size, this can be ascribed to segregation of dwarfing factors in the parent, *e.g.*, in *Crepis tectorum* (Navashin, 1926), where great size variation occurs in the diploid. It may be that in some species giant polyploids are not fitted to survive, and the failure of polyploidy to appear in many groups of flowering plants may be due to failure of such species to segregate or mutate to dwarfness.

TABLE 34

Measurements of Cell Size in Haploids, Diploids, and Polyploids

I. (i) and (ii), *Funaria hygrometrica*, leaf gametophyte (v. Wettstein, 1924). (iii) *Crepis capillaris*, dermatogen (Navashin, 1931 *b*).

	x.	*2x.*	*3x.*	*4x.*
Cell number (i.)	48	49	32	13
Cell volume (ii.)	86·5	158·1	273·1	472·8
Cell volume (in 1,000 cu.μ) (iii.)	1·8	4·0	6·0	9·0

II. *Raphanus-Brassica* hybrids (stomata) (Karpechenko, 1928).

	R. *2x*	*B.* *2x*	*RB.* *2x*	*RRB.* *3x*	*RRBB.* *4x*	*RRRBB.* *5x*	*RRRBBB.* *6x*
Length	7·3	7·1	7·1	9·4	9·7	10·6	10·4
Breadth (in mm. × 1,350)	5·5	5·3	5·4	6·7	7·2	7·8	7·9
Cubical proportion	—	—	1·0	—	2·3	—	3·1

III. *Drosophila* (eye-facets) (Bridges, 1925 *b*). *N.B.*—The triploid is an unrelated individual.

	x.	*2x.*	*3x.*
Linear proportions	1	1·21	1·37
Cubical proportions	1	1·77	2·56

When these observations are compared with similar observations of diploid and polyploid forms of remote origin, whether species or varieties, various kinds of difference are found, which may be classified under three heads.

1. Many polyploid wild species and cultivated forms have the same proportionate increase in size as is found in critical experiments, and it may then be inferred that little change has taken place in the polyploid since its origin. This conclusion is particularly obvious because wild species of this kind are found to be propagated vegetatively or "semi-vegetatively" (*e.g.*, *Vallisneria gigantea*, Jørgensen, 1927 *a*; Caninæ roses, *v.* Ch. XIII), and the cultivated forms have been subject to human selection in favour of size since their origin (*e.g.*, *Triticum* species, Sax, 1922; *Petunia*, Dermen, 1931).

2. Certain polyploid species and races are no bigger, or are even smaller, than their diploid relatives, yet in certain structures such as pollen grains, they preserve what must be supposed to be their initial gigantism. This is true of the Cinnamomeæ roses, where the polyploid species are actually of smaller growth than the diploid (Erlanson, 1932), and of *Primula obconica* (Philp, unpublished) and *Euphorbia granulata* (Hagerup, 1932), where there is no evidence of gigantism in the tetraploid forms except in the size of the cells (*cf.* *Allium*, Levan, 1932).

TABLE 35

Linear Measurements of Cells in Polyploid Derivatives (in microns)

	2x.	*3x.*	*4x.*	*6x.*
Petunia vars., pollen grains . .	35·3	37·6	41·7	—
Triticum species, pollen grains . .	44·0	—	51·1	55·3
Rosa (sect. Cinnamomeæ), pollen mother-cells	6·8	—	8·8	10·0
Primula obconica vars., pollen grains	29·4	—	32·9	—
Allium species, pollen grains . .	29·0	—	35·0	—

3. Finally the great body of polyploid species show a purely random size relationship with their diploid relatives, being on the average neither larger nor smaller as a whole or in any particular structure. Thus Kihara and Ono (1926) found that the size of pollen

grains in *Rumex Hydrolapathum* ($2n = 200$) was no greater than in related diploid and tetraploid species ($2n = 20, 40$).

It is therefore necessary to explain why polyploid species have lost the initial size difference they must be supposed to have had, first in their general structure, and later in their detailed structure. Apart from changes in chromosome number, it is found that the progeny of new allopolyploids vary in fertility (*e.g.*, *Ægilotricum*, Kihara and Katayama, 1931; *Raphanobrassica*, Karpechenko, 1927, *a* and *b*), and in size (*Primula kewensis*, Newton and Pellew, 1929; *Nicotiana digluta*, J. Clausen, 1928). Such changes must be chiefly due to the pairing and crossing-over which must take place occasionally between chromosomes of opposite parents, even with the highest differentiation.

In old established polyploids such as *Triticum vulgare* and *Avena sativa* such abnormalities still occur, and when they occur give rise to variation. An occasional quadrivalent is formed owing to the pairing of dissimilar chromosomes from the ultimate diploid ancestors (autosyndesis) as well as pairing between identical chromosomes. When the dissimilar chromosomes pair, segregation of new types (actually resembling related species) results. This " illegitimate " pairing gives, as we have seen, " secondary segregation," and occurs more frequently in varieties newly derived from crossing different races.

In this way will arise variations on which natural selection can work to change the size of the new form. But such variations will not increase its fertility. Recombination of whole chromosomes or even of any large parts will mean a reduction in the differentiation of opposite sets, tending towards autopolyploidy and hence towards lower fertility. It is therefore probable that the occurrence of structural changes in the two separated sets in the normal course of variation is a more important source of differentiation between the chromosome sets, and thus of the evolution of allopolyploids in general. This will be shown more clearly by considering the occurrence of polyploidy within the species.

(iii) **Polyploidy within the Species.** Many species have been found to include a series of polyploid forms. In some cases these are indistinguishable from one another, except by distribution, while in others they show size differences or slight differences of a general character.

It might be assumed that such polyploid forms had arisen from their diploid relatives within the species, by hybridisation with a second species followed by selective elimination in the polyploid of all the characters of one parent which distinguished it from the other, *i.e.*, *convergence* of the two forms, parent and hybrid.

But it is more plausible to assume that these forms arose as autopolyploids, that is, as giants with free pairing amongst their homologous chromosomes. This condition is still found in certain forms which have presumably remained unaltered since their origin. Amongst these are the sterile polyploid clone-species in *Tulipa*, and probably the giant forms in *Allium* and *Portulaca*.

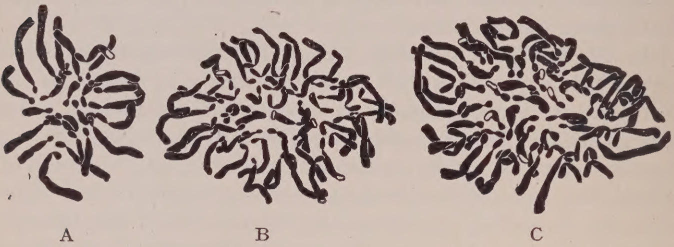


FIG. 62.—Mitotic metaphases from the three clonal types of *Tulipa Clusiana*. A. The diploid from Thibet. B. The tetraploid from Chitral. C. The pentaploid from the Mediterranean. *Cf.* Plate II. (D., unpublished.)

The rest, however, have changed in one or, as in the case of *Silene ciliata* or *Viola Kitaibeliana*, in both of two ways: they have lost their gigantism; they have become allopolyploid. For example, the hybrid between the two forms of the *Viola* species shows no autosyndesis (Table 28). The loss of the gigantism may be attributed to mutation and segregation as already suggested. The loss of the autopolyploidy must be due to differentiation arising between the different pairs of haploid sets. Structural changes in the chromosomes might lead both to the differentiation and to the loss of gigantism; it would be advantageous to any race to have pairs of chromosomes alike in regard to any new structural change, for this would prevent the formation of larger associations of chromosomes than twos. This method of differentiation is probably therefore the chief agent of change in polyploid forms after their origin. It is, in general, analogous in cause and effect to that which arises between particular pairs of chromosomes in sex heterozygotes and between the two whole sets in complex heterozygotes (Ch. XIV).

TABLE 36

Examples of Polyploidy within the Species

A. *Not associated with systematic differences* (other than distribution)

Rosa acicularis Lindl.	*n* = (7), 21, 28	Täckholm, 1922; Erlanson, 1929.
Potentilla opaca L.	*n* = 7, 14	Tischler, 1928.
Callitriche stagnalis	*n* = 5, 10	Jørgensen, 1923.
Salix aurita L.	*n* = 19, 38	Blackburn and Harrison, 1924; Håkansson, 1929 *b*.
Ranunculus acris	*n* = (6), 7, 14	Senjaninova, 1926; Sorokin, 1927; Larter, 1932.
Anemone montana	*n* = 8, 16, 24	Moffett, 1932 *b*.
Nasturtium officinale	*n* = 16, 32 (and 16×32).	Manton, 1932.
Draba magellanica Lam.	*n* = 24, 32, 40	Heilborn, 1927.
Crepis Bungei Ledeb.	*n* = 4, 8	Hollingshead and Babcock, 1930.
Cassia mimosoides	*n* = 8, 16	Kawakami, 1930.
Silene ciliata	*n* = 12, 24, 96	Blackburn, 1928.
Dianthus carthusianorum	*n* = 15, 30	Rohweder, 1929; Andersson and Gairdner, 1931.
D. plumarius	*n* = 15, 45	
D. arenarius	*n* = 30, 60	
Festuca elatior	*n* = 7, 21, 35	Lewitsky and Kuzmina, 1927.

B. *Associated with slight systematic differences* (*cf.* Table 65, Ch. XV, and Table 31, Ch. VII)

Plantago major L., *s.l.*	*n* = 6, 12	Miyaji (*cf.* Ishikawa, 1916).
Papaver nudicaule, *s.l.*	*n* = 7, 35	Ekstrand, 1918; Ljungdahl, 1924.
Erophila verna L., *s.l.*	*n* = 7, 15, 32	Winge, 1926.
Viola Patrini DC., *s.l.*	*n* = 12, 24, 36.	Miyaji, 1913, 1926, 1929.
V. biflora L., *s.l.*	*n* = 6, 24	Miyaji, 1929.
V. Kitaibeliana R. et S., *s.l.*	*n* = 7, 8, *ca.* 12, 18, 24.	J. Clausen, 1927, 1929, 1931 *c*.
Valeriana officinalis L., *s.l.*	*n* = 7, 14, 28	Meurman, 1925; Senjaninova, 1927.
Ranunculus Ficaria	*n* = 8, (9), 16	Larter, 1932.

Vicia Cracca L.	$n = (6), 7, 14$	Sveshnikova, 1928.*
Prunus spinosa	$n = 8, 16$	D. 1928, 1930 *a*; Mather, unpublished.
P. domestica L., *s.l.*	$n = 8, 24$	
Rosa blanda	$2n = 14\ (16), 45\ (= 6x +)$.	Erlanson, 1929, 1931.
Lythrum Salicaria	$n = 15, 25$	Tischler, 1928, 1929 *b*; Shinke, 1929.
Solanum nigrum, *s.l.*	$n = 12, 24, 36$	Vilmorin and Simonet, 1928.
Biscutella lævigata	$n = 9, 18 +, 27$	Manton, 1932.
Dianthus superbus	$n = 15, 30$	Rohweder, 1929; Andersson and Gairdner, 1931.
Portulaca oleracea	$n = 9, 27$	Hagerup, 1932.
Euphorbia granulata	$n = 10, 20$	Hagerup, 1932.

2. THE INFERENCE OF POLYPLOIDY

(i) Statistical Evidence. Winge (1917) was the first to point out that the high frequency of multiples and low frequency of primes among the gametic chromosome numbers of the flowering plants might be taken to show that polyploidy was a common source of new species amongst them. New data have been examined from this point of view by Fernandes (1931), who has shown that in the frequency graph of numbers between 3 and 100 (the highest number considered) not a single peak is found at a prime number. Further, the most important peaks are at the numbers with the lowest factors, *viz.*, 8, 12, 16, 24, 27, 32 and 36. This means that these numbers are favoured by the conditions of origin or survival of new forms; such would be the case if they owed their origin largely to a process of reduplication which gave in the first instance doubling, in the second instance trebling, quadrupling, and so on; in a word, to polyploidy.

This conclusion is supported by the observation of polyploid behaviour of various kinds in nearly all species with these higher numbers, but it is not supported by observations on species with 8 chromosomes or, for the most part, on species with 12 (*cf. Nicotiana*,

---

* Three geographical races of *Vicia Cracca* are found (Sveshnikova, 1928) with 12, 14 and 28 chromosomes. The 12-chromosome race differs from the 14-chromosome race in having two short pairs in place of the one long one (*v.* Fig. 12). The 28-chromosome race has the complement of the 14-chromosome race represented twice except that one pair have lost their trabants, an indication that secondary changes (such as deficiencies and translocation) have taken place in the polyploid since its origin. The same combined differences are found in *Ranunculus acris*, *R. Ficaria* and *Crocus vernus* (Mather, 1932).

Ch. IX). The discrepancy is important, for it indicates that many of these were polyploid in origin but have since lost all trace of their origin, except in their number, through later differentiation of the kind already discussed.

Fernandes' enumeration is summarised in the following list. It is chiefly derived from the lists compiled by Tischler (1926) and Gaiser (1930). It is a fairly random sample embracing records of 2,413 species. The most abundant contributors have not always been the most exact, but there are probably less than 5 per cent. of erroneous observations included.

TABLE 37

Chromosome Numbers in the Phanerogama

Chromosome number.	Number of species.	Chromosome number.	Number of species.
12	391	5	27
8	332	15	27
7	236	22	25
9	170	32	25
16	153	28	24
6	134	19	22
10	126	26	20
14	125	36	19
24	80	30	11
11	70	23	8
21	64	45	8
18	58	42	6
17	48	3	5
20	47	38	5
4	42	40	5
27	31	Rest	39
13	30		

Totals:		
Totals:	Below 12	1,242
	12 and above	1,171
	Altogether	2,413

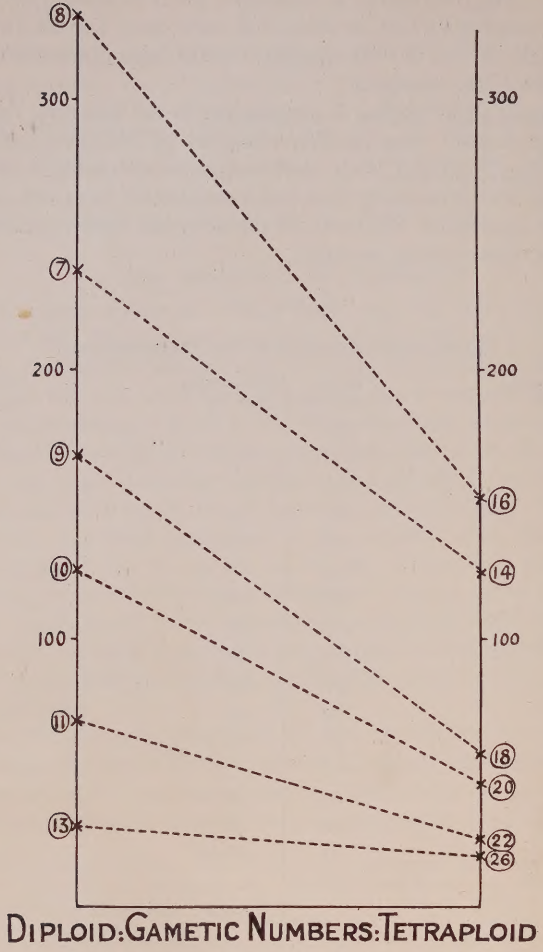


FIG. 63.—Graph showing the relationship between the numbers of species having certain low haploid numbers and the numbers of species having twice as many chromosomes. (From Table 37.)

In order to find out the relative importance of polyploidy and other changes in chromosome number, these records may be examined from a different point of view. There are certain numbers between 6 and 12 and the number 13 which can but rarely be regarded as having arisen from recent polyploidy. The number of species of each of these classes proves to have a definite relationship with the number of those having double the number. Fig. 63 represents graphically the results of the comparison. Three inferences can be drawn from this: first, that the double numbers owe their origin chiefly to polyploidy; secondly, that change in the basic number is, relative to change by doubling, somewhat rare; and thirdly, that no differential elimination of forms with certain numbers has occurred, as it might, owing to some numbers being more suitable mechanically than others. These conclusions are already probable on experimental grounds, for polyploidy is the most frequent of all changes observed in plant species (*cf. Crepis*, Table 10).

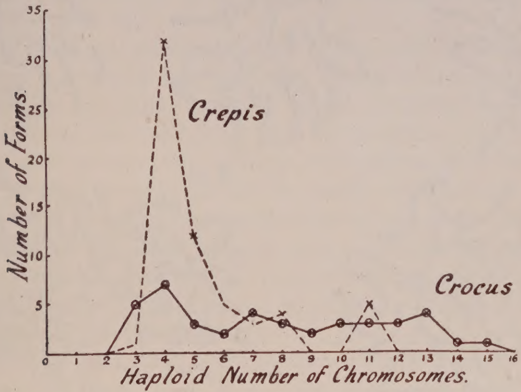


FIG. 64.—Graph showing the distribution of species with different numbers of chromosomes in *Crepis* and *Crocus* where polyploidy has played little part in the change in numbers. *Crocus* can be regarded as having the same type of differentiation as *Crepis*, but at a more advanced stage of development. (From Mather, 1932, *cf.* Fig. 16.)

When the species of smaller systematic groups are considered, differences are found both in the amount and in the kind of variation in chromosome number. Some large groups are found to show no variation (Ch. III). Others show the influence of the polyploid series in various degrees. The graph (Fig. 64) of variation in number in *Crepis* (Babcock and Navashin, 1930), and *Crocus* (Mather, 1932) illustrates types where polyploidy has played little part. *Crepis* is more constant than *Crocus*, for it has a high proportion with the number four which must be considered the original number of the genus. In *Crocus* the distribution of numbers is almost at random. How far the changes responsible are merely numerical, *i.e.*, due to changes in the numbers of certain chromosomes, and how far they are structural, *i.e.*, due to fragmentation and fusion,

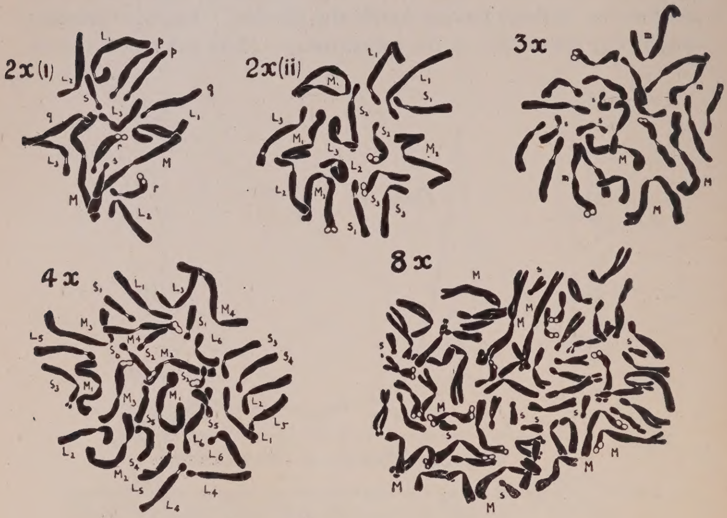


FIG. 65.—Mitotic metaphases in *Aconitum* ($x = 8$) diploid and tetraploid species, a triploid clone and an octoploid giant variety. The chromosome types are reduplicated in the forms with higher numbers. $2x$ (i) *A. barbata.* $2x$ (ii) *A. vulparia.* $3x$ *A. Napellus*, "Spark's Variety." $4x$ *A. anglicum.* $8x$ *A. volubile latisectum.* × 2000. (D., unpublished.)

can only be said after a detailed study of meiosis in hybrids. But there is clearly a similar variety of species in the two genera with less variation in chromosome number in *Crepis* than in *Crocus*. This is probably due to the greater importance of sexual reproduction (and therefore of regularity at meiosis) in the one than in the other.

Crepis and *Crocus* approach the distribution of numbers found in animals where there is no evidence of polyploidy. The opposite extreme is found in genera such as *Chrysanthemum*, *Triticum*, *Rosa*, *Solanum* and *Aconitum*, where all species have multiples of a common basic number (Fig. 65).

(ii) **New Polyploid Species.** Clearly it can only be possible to reconstruct the method of origin of a species when it has arisen fairly recently. Suitable conditions could probably be found to allow of several new polyploids that have arisen in experiment becoming wild species. But amongst wild species there are a few the conditions of whose origin can be stated with precision. First there are those giant varieties found within species (Table 36) which can certainly be supposed to have arisen from simple doubling. Similarly, *Vallisneria spiralis* ($n = 10$) is diœcious, and appears to have given rise to *V. gigantea* ($n = 20$) of both sexes separately by somatic doubling (Jørgensen, 1927).

Secondly, there are allopolyploid species whose diploid parents are known with certainty. Thus the new artificial tetraploid *Galeopsis* is indistinguishable from *G. Tetrahit*. The hexaploid *Phleum* is indistinguishable from the American species, and *Spartina Townshendii* is systematically intermediate between the two species from which it was believed to have arisen and its chromosome number if the sum of theirs. Similarly, the chromosomes of the reputed parents of *Æsculus carnea* can be recognised in the hybrid (Fig. 66).

Amongst cultivated plants there are also many forms of equivalent rank to new species, whose origin can be inferred with high certainty. Such are the autopolyploid *Petunia* varieties (Denman, 1930) and certain allopolyploid *Rubi* (Crane and D., 1927).

In all these cases, therefore, there can be no doubt that a new species has been produced in one generation. This is possible with polyploidy and also with other changes which are in themselves of greater evolutionary significance. Some of these will be discussed in regard to mutation in *Œnothera* (Ch. XIV).

TABLE 37A.

Allopolyploid Species whose Origin can be Determined

Genus	Species	Hybrid
1. *Æsculus* (10)	*Hippocastanum* ($4x$) × *pavia* ($4x$)	= *carnea* ($8x$), Skovsted, 1929 (Fig. 66).
2. *Galeopsis* (8)	*pubescens* ($2x$) × *speciosa* ($2x$)	= *Tetrahit* ($4x$), Müntzing, 1927, 1930 *b*.
3. *Phleum* (7)	*pratense* ($2x$) × *alpinum* ($4x$)	= *pratense* (America), ($6x$), Gregor and Sansome, 1930.
4. *Spartina* (7)	*alterniflora* ($10x$) × *stricta* ($8x$)	= *Townshendii* ($18x$), Huskins, 1930.

(iii) **Somatic and Secondary Pairing.** At metaphase of mitosis the spindle attachment of each chromosome lies in the equator of the spindle. Apart from this the position of the chromosome as a whole is at random with regard to the spindle, so that if the chromosome is long its distal parts may be well to one side of the equator and well away from the spindle—being actually seen to move in the currents of protoplasm outside. But the chromosomes never seem to touch one another, and the limbs of those on the outside of the spindle turn outwards. Further, the chromosomes, as wholes, are distributed evenly on the equator so far as their spindle attachments allow them to be. These three rules, which apply equally to meiosis, argue a strong repulsion between the spindle attachments and a weak repulsion between the bodies of the chromosomes.

But in some organisms the even distribution is modified. At mitosis in the diploid in many Diptera, pairs of chromosomes are seen to lie specially close together, although still never touching, and these are found to be similar pairs, with similar parts lying parallel. The fact that this is particularly noticeable in Diptera is partly due to the favourable conditions of small number and distinct shape of chromosomes, but also probably to a specially exaggerated property of such association in this group (*cf.* Metz, 1923, 1926 *et al.*; also Fig. 14). The same "somatic pairing" has been found between the chromosomes of polyploid plants at mitosis (*e.g.*, *Dahlia*, Lawrence, 1932). In this case more than two chromosomes being attracted to one another, the groups lie radially instead of parallel.

More striking, however, are the conditions in tetraploid nuclei which have probably arisen in diploids through the failure of the chromosomes to separate at the preceding division (*e.g.*, *Spinacia*, Stomps, 1911 ; *Sorghum*, Huskins and Smith, 1932). Probably in these the daughter chromosomes have remained together during the resting stage, and have therefore been in a suitable position to exercise their special attraction on one another during the prophase. At metaphase every pair is distinguishable by the chromosomes being of similar shape and lying parallel. This is evidence not only of the method of origin of polyploid nuclei, but also of the static condition of the chromosomes during the resting stage, and of their affinity at metaphase.

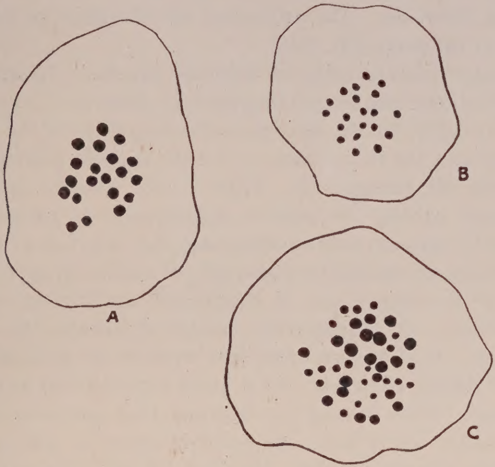


FIG. 66.—First metaphase of meiosis in Æsculus. A. *A. pavia*, $n = 20$; B. *A. Hippocastanum*, $n = 20$; C. *A. Carnea*, $n = 40$. The bivalents show secondary pairing both in the parents and in the hybrid. × 2400. (From Skovsted, 1929.)

The special attraction of chromosomes seems to be specific to their parts, since it leads to the corresponding parts lying parallel ;

and Sturtevant and Dobzhansky (1930) find that the four chromosomes in an interchange heterozygote in *Drosophila* lie in a ring at mitosis. Stern (1931), on the other hand, finds no evidence of attraction of the distal end of a normal *X* for the corresponding translocated part of its homologue. If, however, the attraction is not specific to the parts of chromosomes, it must be a property of the spindle attachment. Such specificity of the spindle attachment is not paralleled and does not account for the attraction of parts observed elsewhere. The attraction will therefore be taken to be specific to the parts (Ch. XII).

A similar juxtaposition of different bivalent chromosomes at meiosis has long been known in polyploid plants (*cf.* Kuwada, 1910 ; Ishikawa, 1911), but its relation to the homology of the associated bivalents and its independence of true meiotic pairing was not recognised till recently (D., 1928). Like somatic pairing, this " secondary pairing " is between chromosomes of similar size and shape and it appears first at metaphase, *i.e.*, it is not a continuance of a prophase association by chiasmata ; it consists in approximation, but never in contact, *i.e.*, it reaches an equilibrium with forces of repulsion ; it consequently cannot determine the anaphase separation. It is, in fact, continued between the pairs of daughter bivalents during anaphase, and is often most marked at the second metaphase. Thus it may be supposed that whatever attraction is responsible for it has a cumulative effect in sorting out the homologues during the two divisions. Again, like somatic pairing, it is variable in its occurrence from division to division. Cytologists have usually illustrated the nuclei that were freest of it, to avoid the suspicion of bad fixation, and in consequence its occurrence has been generally neglected, as Lawrence (1931) has pointed out in a general review of the problem. Secondary pairing, like many peculiarities of chromosome behaviour, is exaggerated in appearance by bad fixation, but its essentially differential character as between different chromosomes cannot be determined by an external agent—it is not an artefact (*cf.* Kihara, 1927 *b*).

How is it that somatic pairing does not show itself at mitosis in organisms with secondary pairing at meiosis ? The answer to this question is clearly that the chromosomes in a somatic mitosis

PLATE V

SECONDARY PAIRING AT MEIOSIS IN POLYPLOIDS

FIG. 1.—*Cydonia cathayensis* (Pomoideæ), $2n = 17$.

FIG. 2.—*Pentstemon lævigatus*, $2n = 96 = 12x$.

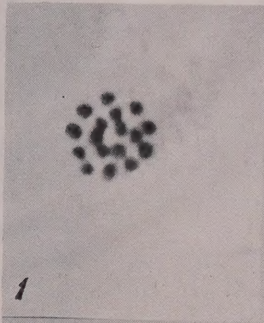
FIG. 3.—*Dahlia coronata* × *D. coccinea*, $2n = 32 = 4x$.

FIG. 4.—Second metaphase in *Prunus cerasus*. $19 + 13$ chromosomes. $2n = 32 = 4x$ (*cf.* D., 1928).

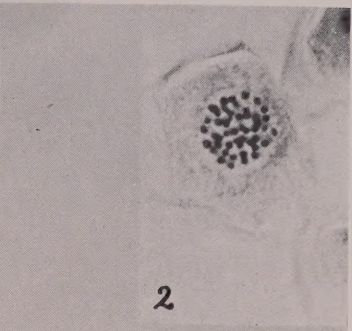
FIGS. 5 AND 6.—*Dahlia variabilis*, the same plate at two focuses. $2n = 64 = 8x$.

Figures reproduced by kind permission of Mr. A. A. Moffett (Fig. 1), Mr. L. La Cour (Fig. 2), and Mr. W. J. C. Lawrence (Figs. 3, 5 and 6).

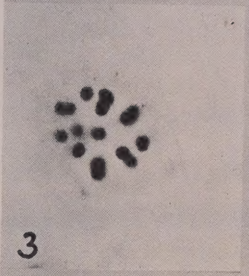
PLATE V



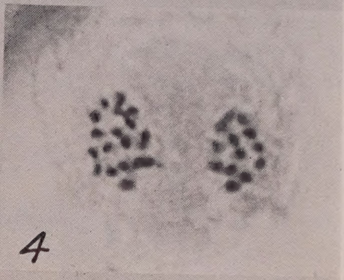
1



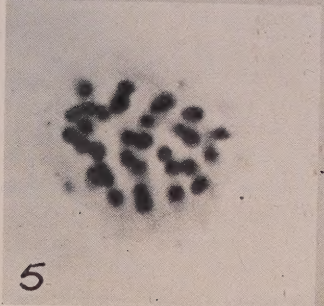
2



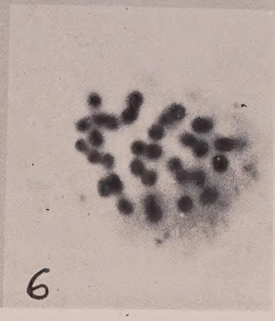
3



4



5



6

[To face p. 220.

are always widely distributed, while at the end of diakinesis (" pro-metaphase " of meiosis), when secondary pairing begins, they are brought within close range of one another, and therefore on analogy should attract one another more strongly. Further, they are spherical at meiosis, and so should oppose less resistance to movement through a viscous medium than when they are long, as in mitosis (Lawrence, *l.c.*). Secondary pairing is not found at meiosis in plants whose chromosomes are still long at this stage (*e.g.*, in *Tulipa*).

Secondarily paired bivalents are distinguished from multivalents associated by chiasmata in four ways: (i) they lie evenly side by side, in twos, threes or larger groups according to whether the plant is a tetraploid, hexaploid or higher polyploid; (ii) they never touch, except through collapse in fixation; (iii) they separate regularly into their daughter halves without interfering with one another; (iv) they show no association at the preceding diakinesis (D., 1928; Lawrence, 1929).

The distinction has a profound theoretical importance. It has been generally held that the characteristic pairing of chromosomes at meiosis was merely an exaggeration of the somatic pairing observed at mitosis. But chiasma pairing and " somatic " pairing are now seen side by side at meiosis, and the differences in their effects are as clear as the differences in their causes. These will be discussed later (Chs. XI and XII). In many polyploid species, where the two phenomena occur side by side, it is of great importance for genetic interpretation to tell one from the other, for chiasma pairing indicates a closer relationship than secondary pairing. It will have been seen that, while the separation of diploid and polyploid is a convenient one, every possible degree of relationship must be found within the gametic sets of different organisms. There must be polyploids so ancient that the original relationship between their chromosomes has been lost so far as pairing analysis can reveal it. There must also be diploids having parts of their chromosomes reduplicated, and therefore having internal relationships not unlike those of polyploids. In fact, the behaviour of haploids, with other considerations, makes it probable that this is true of all diploids in varying degrees (*v.* Ch. IX). It follows, therefore, that all slight unevennesses of distribution of chromosomes on the metaphase plate might conceivably be interpreted in terms of genetical relationship if they could be measured sufficiently accurately. This is of practical importance in the analysis of polyploidy. Most ordinary cases are clear enough from purely numerical considerations, but where no species is known with a lower basic number or where the number is not a simple multiple, the evidence of secondary pairing becomes of use. The distribution of chromosomes on the equatorial plate may be used to show relationships between them, or, more exactly, between some of their constituent genes, which are beyond analysis by the two other methods—comparison of shape at mitosis

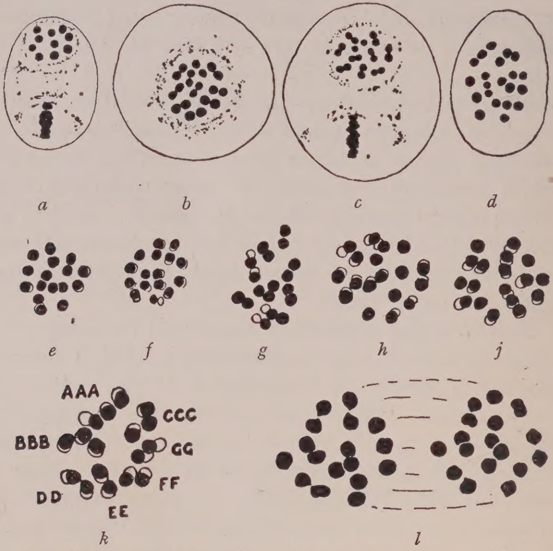


FIG. 67.—Secondary pairing at meiosis in the pollen mother-cells. *b* and *e* to *k*, first metaphase; *l*, first anaphase; *a*, *c* and *d*, second metaphase. *a*, *Euphorbia scordifolia* ($2x = 20$). *b*, *c*, *E. granula* ($4x = 40$). *d*, *Rubus* "Loganberry" ($6x = 42$). *e*, *f*, *Dahlia coccinea* ($4x = 32$). *g*, *h*, *j*, *D. Merckii* ($4x + 4 = 36$). *k*, *l*, *Pyrus Malus* ($4x + 6 = 34$). *a* to *c*, after Hagerup, 1932; *d*, from Crane and D., 1927. *e* to *j*, from Lawrence, 1929 and 1931. *k* and *l*, from D. and Moffett, 1930, and Moffett, 1931.

or frequency of chiasma formation at meiosis. The application of this method will now be considered.

(iv) **Secondary Polyploidy.** Since new polyploids when they are hybrid already behave at meiosis to a great extent like diploids, it follows that polyploid species which have changed since their origin can be identified only by more or less circuitous inferences. And although such inferences can be drawn without much hesitation for the bulk of species in the angiosperms, there remains an interesting group of doubtful cases.

Where, as in one section of *Rumex*, species occur with " haploid " or gametic numbers of 10, 20, 30, 40, 50, 60 and 100, and the chromosomes are comparable in size, it is natural to assume without further evidence that the higher-numbered species arise through multiplication of a " basic " set of 10 chromosomes such as that found in the lowest-numbered ones. The inference is less direct in such genera as *Dahlia* ($n = 16, 32$) and *Digitalis* ($n = 28, 56$). These numbers are multiples respectively of 8 and 7 which are found in related genera. The conclusion that 8 and 7 are the basic numbers, however, requires the support of other evidence. Still less direct is the inference in those genera in which uneven multiples occur. Many of these, such as *Brassica* ($n = 9, 10, 17, 18, 19$) and *Papaver* ($n = 7, 11$), are not yet elucidated, and in the hybrid *Nicotiana longiflora* (10) × *N. alata* (9) ($9^{\text{II}} + 1^{\text{I}}$, Goodspeed and Clausen, 1927 *b*), it is not clear whether the extra chromosome arises from fragmentation or reduplication. Others can be understood as the result of fusion between non-homologous chromosomes after the occurrence of polyploidy. Thus *Cardamine pratensis* (Lawrence, 1931, $n = 15$) is a tetraploid with an original basic number of 8, two chromosomes having fused, and *Nicotiana longiflora* ($n = 9$) is probably derived by fusion from a species with a haploid number of 12 (Ch. III). Others, again, show no evidence of fusion or other structural change, and it would appear that they result from the unbalanced multiplication of the basic set, two or three of the chromosomes occurring once more often than the rest. It is in relation to these supposed " secondary polyploids " that the criteria of polyploidy require to be strictly examined.

The evidence has been most fully adduced in the Pomoideæ section of the Rosaceæ (D. and Moffett, 1930 ; Moffett, 1931, *a* and in which it is assumed that a chromosome set of 17 (and its multipl found throughout the section is derived from the set of seven fou in other sections of the order (*e.g.*, in *Rosa* and *Rubus*) by unequ reduplication, so that the seven chromosomes *A* to *G* are present the proportions

$$AAA, BBB, CCC, DD, EE, FF, GG,$$

making up 17 in all.

The evidence, chiefly from *Pyrus*, is of the following kinds :—

(i) *Occasional quadrivalents* are found in the diploid with normal 17 pairs. (These might also result from interchange hybridity.)

(ii) *Secondary pairing* reaches its maximum in the appearan of seven groups of bivalents, three groups of three, four of tv (Fig. 67).

(iii) In non-hybrid " triploids " (with 51 chromosomes), *au syndesis* occurs in the third set of 17, so that more than 17 pairs m be formed (Nebel, 1929); and multivalents up to 9 chromosom are formed (*v.* Fig. 56).

(iv) The progeny of triploids back-crossed with diploids, inste of showing the elimination of types with intermediate numbers that most of the seedlings have approximately the diploid numb show the highest frequency with 41 chromosomes (*i.e.*, the seconda diploid number, 34, together with the primary basic number This indicates that the original *balance* of 7 still has a certa vestigial significance (*v.* Ch. IX).

(v) The somatic complement includes *four* chromosomes of o exceptional type, as is found in tetraploids.

(vi) Genetic evidence indicates more complex conditions th those found in strictly diploid fruits.

In the Pomoideæ the inference of polyploidy is necessarily t most indirect, since the original change from 7 to 17 by which su an important group arose must have occurred at an epoch mo remote than any on which inference can usually be brought bear. In another group, however, the case is simpler. *Dahl Merckii* has 18 haploid chromosomes (Lawrence, 1929), while other species of *Dahlia* have multiples of eight. The occurrence secondary pairing agrees with the assumption that two of the eight chromosomes are present three times, while the rest are present twice (Fig. 67).

Chromosome pairing in certain hybrids suggests that reduplication of part of the set is responsible for the origin of new complements in *Brassica* and *Papaver*, and perhaps *Viola*, but no final conclusion can be drawn in these cases.

Brassica cernua ($n = 18$, $4x$) × *B. chinensis* ($n = 10$) and other species : $10^{\text{II}} + 8^{\text{I}}$ (Morinaga, 1929).
Papaver somniferum ($n = 11$) × *P. orientale* ($n = 21, 6x$) : $11^{\text{II}} + 10^{\text{I}}$ (Yasui, 1921 ; Ljungdahl, 1922).
Viola tricolor alba ($n = 13$) × *V. elegantula* ($n = 10$) : $8\text{–}10^{\text{II}}$, $7\text{–}3^{\text{I}}$ (Clausen, 1931 *c*).

The distinction between secondary polyploidy and structurally changed polyploidy (*i.e.*, polyploidy followed by fragmentation or fusion) is important, because the first means an important change in genetic balance, while the second means little or no change of this kind. On the analogy of most trisomic and tetrasomic forms a polyploid with a new balance will, if it breeds true, constitute a new species. The Pomoideæ are a sharply characterised group of the Rosaceæ and *Dahlia Merckii* is the most sharply characterised species of *Dahlia*.

The types so far elucidated are unbalanced modifications of tetraploids, not of diploids. It may be supposed on analogy that tetrasomic diploids would as a rule be sterile, the unbalance being too drastic. This is true also of artificial secondary polyploids.

A secondary polyploid form has been produced in experiment in *Nicotiana* in the following way. From a pentaploid having the complete complement of *Nicotiana Tabacum* ($4x = 48$) given by an unreduced gamete together with a haploid set of *N. sylvestris* ($2x = 24$), a plant was derived in F_6 having fifty chromosomes forming $2x + 1$ pairs (Webber, 1930). This is potentially capable of breeding true and has a combination of characters distinct from that of any of its progenitors.

Similarly, from the cross between the probably autopolyploid *Crepis biennis* ($2n = 40 = 8x$) and the diploid *C. setosa* ($2n = 8$) it has been possible, owing to autosyndesis, to derive a new true-breeding form, "*Crepis artificialis,*" having ten pairs of chromosomes from *C. biennis* and two from *C. setosa* (*cf.* Table 28). This new form is balanced in its *biennis* fraction, unbalanced in its *setosa* fraction (lacking 2 pairs of chromosomes). It therefore has the constitution of a secondary polyploid.

These experiments show how secondary polyploidy may be supposed to have arisen in *Dahlia* and in the Pomoideæ, viz., in the derivatives of crosses between original polyploid forms with different numbers of chromosomes. Thus selfing a pentaploid, derived from crossing a tetraploid and hexaploid would give, in the *Rosa* type with seven chromosomes, trisomic and tetrasomic seedlings with numbers between 28 and 42. The latter, if they bred true, would be secondary polyploids.

Further investigation will probably show that secondary polyploidy, and other variations due to change in balance (such as reduplication of segments), is an important source of species-formation in plants. Secondary pairing indicates such an explanation of the origin of the chromosome complements in many genera with basic numbers of 13, 17 and 19 (*e.g.*, *Empetrum*, *Gossypium*, *Salix*; *cf.* Lawrence, 1931).

CHAPTER IX

THE CHROMOSOMES IN HEREDITY. PART I

The Chromosome Theory—Qualitative Differentiation—Balance—Intra-Haploid Homology—Secondary Balance—Evidence of the Gene—Segregation.

> Besonders aussichtsreich scheint mir gerade bei diesem Problem, dass wir ihm gewissermassen von zwei Seiten her beikommen können, einmal durch die Beobachtung der Vererbungs-Erscheinungen und dann durch die Beobachtung der (uns jetzt ja bekannten) Vererbungs-Substanz.
>
> WEISMANN, 1892.

1. THE CHROMOSOME THEORY OF HEREDITY

THE chromosome theory of heredity is the hypothesis (and the corollaries of the hypothesis) that :—

> the permanence of the physiological properties of organisms which is manifested in heredity is determined by the permanence in the structure of their chromosomes.

In order to examine the theory it is necessary first to recall the special properties associated with heredity and shown by genetical analysis, *i.e.*, by the comparison of parents and their offspring in their *super-genic* organisation.

They may be conveniently arranged under five heads, as follows :

1. *Potential Permanence.* Heredity consists in the same character being reproduced in successive generations ; a causal explanation, therefore, requires the assumption of permanence in the cause, although, since the character is only *liable* to be reproduced, the permanence is only potential. Potential permanence has already been shown to be a universal property of the chromosomes (Ch. II).

2. *Qualitative Differentiation.* Every organism has various and specific properties of variation (mutation) which are also permanent ; the permanent material must therefore be of various specific kinds, *i.e.*, must be qualitatively differentiated.

3. *Segregation.* All organisms with sexual reproduction have two stages in their life cycle, the one in which two corresponding

elements or "genes" in each cell affect each character (one from the mother, the other from the father), and the other in which only one of these genes affects each character. There must therefore be a point in the life cycle at which corresponding elements separate or segregate to different daughter cells having half the number present in the mother-cells, as well as a point at which the elements recombine.

The general evidence that separation occurs at meiosis has been given. Since the chromosome pairs which segregate at random at meiosis give corresponding products yet are qualitatively differentiated, it follows that the members of each pair correspond. The recombination is seen to take place at fertilisation (Ch. I).

4. *Linkage.* The elements or genes having different effects are arranged in groups which segregate at random as between groups but with restricted freedom within the group. The restriction, known as linkage, is fixed in degree as between particular genes. It can be represented as fixed by their arrangement in linear order in a thread which has a fixed chance of exchanging segments (crossing-over) with the corresponding thread. The hereditary materials must give evidence of this character and behaviour. The linear character has already been shown of the chromosomes in considering the prophase of mitosis and meiosis.

5. *Mutation.* The elements or genes must be capable of changes affecting their individual properties (gene or point mutation) and affecting their numerical proportions and arrangement (deficiency, translocation, etc.). These structural changes in the chromosomes have been shown (Chs. III, V). The existence of qualitative differences between genes in the same complement is evidence of gene-mutation on an evolutionary hypothesis (Ch. XVI).

Some of the principal evidence for regarding the chromosomes as containing the hereditary materials has therefore already been given. The most unequivocal test of the chromosome theory, or indeed of any theory, is by the verification of prediction. It is possible to base prediction of chromosome form and behaviour on observations by genetical methods, and *vice versâ*, and these predictions can afterwards be tested. Thus it is possible in the case of certain flies mosaic for male and female characters to say that one *X* chromosome has been lost in the course of a somatic mitosis (Stern, 1927). It is possible to say in the case of seedlings such as those raised from the cross *Rubus rusticanus* by *R. thyrsiger* or from natural seed of the *Raphanus-Brassica* hybrid (Ch. VII) that some have one set of chromosomes more than others. These are predictions based on genetical evidence and they have been verified cytologically. On the other hand, it is known that meiosis occurs in the formation of spores of mosses and ferns, and that the gametophytes raised from them are haploid: they should therefore show the 1 : 1 segregation in haploid characters which Mendel supposed was the basis of the 3 : 1 segregation in the diploid generation. These are predictions based on cytological principles and they have been verified genetically (v. Wettstein, 1924; Andersson, 1929). Tests of this kind will be described where they affect debatable points, but in regard to the chromosome theory in general, they are too numerous to be recapitulated here. They have been dealt with elsewhere (Stern, 1928; Sansome and Philp, 1932).

More important, for our present purpose, is the showing of a parallelism between the rules of heredity and the rules of chromosome behaviour, for this parallelism is a help in directing enquiry. Bearing in mind this distinction, we will now consider the evidence as affecting (i) qualitative differentiation, (ii) segregation of homologous chromosomes, and (iii) crossing-over.

2. QUALITATIVE DIFFERENTIATION OF THE CHROMOSOMES

(i) Evidence from Meiosis. The qualitative differentiation of the chromosomes is shown by their specific pairing properties at all stages of meiosis. It was first found by Sutton and Montgomery that particular chromosomes paired at meiosis, and that these chromosomes were similar in size and shape. This meant that the different chromosomes showed specific and different affinities at meiosis. Then it was found that in fusion-heterozygotes (McClung) and interchange-heterozygotes (Belling) each part of a compound chromosome similarly had specific properties. This rested on metaphase observations. Later the development of the structures seen at metaphase was traced back to the diplotene (Gairdner and D., 1931) and pachytene (McClintock, 1931) stages. The specificity was seen to apply to the smallest visible elements, the chromomeres, when zygotene pairing was studied in polyploids, for successive chromomeres, distinguishable in size, could be seen to pair independently of their neighbours when they had a choice of association (Newton and D., 1929) (*v.* Ch. XI).

(ii) Balance. Boveri showed from experiments on doubly fertilised sea-urchin eggs that all the chromosomes making up the complement of a gamete must be present for the normal development of the zygote. He therefore properly inferred that the chromosomes of the complement were qualitatively different.

The same conclusion may be derived from recent experiments of various kinds, some of which carry us much further.

(*a*) MONOSOMICS. The first kind of evidence is derived from organisms which lack either a part or a whole of one chromosome of their diploid complement. The first are said to have a sectional deficiency ; they are deficiency-heterozygotes. The second are said to be " monosomic ; they are numerical hybrids."

Such organisms have arisen in all the conceivable ways, as follows :—

1. Through loss of one chromosome in a somatic mitosis of a diploid, *e.g.*, *Datura Stramonium*, Blakeslee and Belling, 1924 ; *Zea Mays*, McClintock, 1929 *b* ; *Œnothera*, Michaelis, 1926.

2. Through parthenogenetic development of an " unreduced " egg (Ch. XIII) which has lost one chromosome at meiosis, *e.g.*, *Œnothera Lamarckiana* in a cross with *Œ. longiflora*, Stomps, 1931.

3. Through functioning of a deficient egg cell ($x - 1$) in an animal (*e.g.*, *Drosophila melanogaster* giving the haplo-IV type, Fig. 14) or in a plant (*e.g.*, *Nicotiana alata*, Avery, 1929 ; Goodspeed and Avery, 1929 *a*). This is also possible in regard to a segment, as in *Matthiola* heterozygous for lack of a trabant (Philp and Huskins, 1931) which transmits the deficient chromosome through the eggs but not through the pollen, and consequently, when selfed, yields 50 per cent. of offspring heterozygous for the deficiency and none homozygous.

4. Through functioning of a deficient male gamete ($x - 1$) in an animal, *e.g.*, *Drosophila melanogaster*, whose sperm will function lacking an X chromosome (Kuhn, 1929 *b*). In special circumstances

this can occur in plants. Thus Stadler (1931) obtained $2x - 1$ plants by X-raying pollen of *Zea Mays*. Such deficient pollen never functions in competition with normal haploid pollen, and as a rule where it is known to be regularly formed at meiosis (as in ring-forming *Rhœo* and *Œnothera*; *cf.* D., 1929 *c*, 1931 *b*) it never reaches its first gametophytic mitosis. An $x - 1$ pollen-grain division has, however, been found in *Uvularia* (Belling, 1925 *c*).

These observations show that while embryo-sacs and animal gametes may function while lacking a part of the haploid complement (on account of their very limited activities) the male gametophyte of plants is usually incapable of development in this condition. Further, the zygote of plant or animal can never develop when lacking either a section or a whole chromosome of one type entirely, *i.e.*, in both sets. When they are lacking merely in one set, the organism is slower and poorer in development where a section or a small chromosome is concerned, and non-viable where a larger element is concerned, *e.g.*, one of the large autosomes in *Drosophila*.

The fact that a certain group of materials is necessary for the successful working of the life processes enables us conveniently to define the haploid complement of an organism as the minimum combination of chromosomes or parts of chromosomes necessary in

TABLE 38

Distribution of Chromosomes at Meiosis in Triploids

Nos. of chromosomes	6	7	8	9	10	11	12	13	14	15	16
Hyacinthus (pollen grain) $x = 8$. Belling, 1925; D. 1926			4	28	61	91	88	69	33	5	2
Tradescantia (pollen grain) $x = 6$. D., 1929 *c*	—	4	13	30	21	4	—				
Petunia (second metaphase) $x = 7$. Dermen, 1931		1	12	32	40	41	20	5	1		

Note.—The slight excess of the numbers below $3x/2$ is due to loss of chromosomes at meiosis.

single or double number for the development of the organism to maturity.

(*b*) Progeny of Triploids. The second kind of evidence is to be derived from the progeny of triploids. In these the extra chromosomes are distributed at random at the first and second divisions (with slight loss through lagging), and therefore gametes are produced with an approximately binomial frequency of chromosomes ranging from the haploid to the diploid number.

It might be expected from these observations that the progeny of triploids would for the most part receive from their parents approximately $3x/2$ chromosomes.

The zygote progeny, however, do not correspond at all with the gametic proportions. They show a different range according to whether the triploid is the male or the female parent, or both, and whether the opposite parent is diploid or tetraploid. In all these types of cross there is elimination of gametes and zygotes having extra chromosomes. In consequence triploids show a sterility which increases with the number of chromosomes in the haploid set, other things being equal. This elimination depends, first, on a failure of growth of abnormal pollen grains, which is sometimes complete and sometimes merely a failure to compete with normal ones—or with better suited ones, since the diploid pollen of a triploid *Œnothera* grows better on the tetraploid stigma and the haploid pollen on the diploid stigma (Table 39). Secondly, it depends on competition between zygotes in the embryonic stage; this applies equally to the seed of *Solanum* and the larva of *Drosophila*.

Similar elimination is found in the breeding of plants and animals that are simply trisomic, either in a whole chromosome or in part of a chromosome (*v.* Tables 40 and 41) or in the development of pollen of plants of these types (*v.* Table 42).

The different kinds of progeny whose relative viability may be tested differ from the normal in two ways:—

(i) in the size of the fraction of the whole complement which is present in excess, the fraction being in the following degrees: fragment or small chromosome, whole chromosome, two chromosomes, etc.;

(ii) in the disproportion of the excessive fraction to the rest, the proportions being 3 to 2 (trisomic diploid) and 4 to 2 or 2 to 1 (tetrasomic diploid and disomic haploid).

They also differ at different stages of the life cycle owing to differences in the stringency of conditions of life.

Thus the observations on fertility of numerically abnormal zygotes may be used to measure elimination on three scales. Taking the last first, the stringency of elimination increases in the following series : Animal egg, animal sperm, embryo-sac, pollen, plant or animal zygote. Taking the size of the fraction : the higher the proportion of the haploid complement reproduced in excess (up to one-half) the greater the reduction of viability. Taking the disproportion of the excessive fraction : the higher the disproportion the more aggravated is the defect produced.

TABLE 39

Transmission of Extra Chromosomes of Triploids to their Progeny

	$2x$	$2x+1$	$2x+2$	$2x+3$	$2x+4$	$2x+5$	$2x+6$	$2x+7$
$3x \times 2x$ (*i.e.*, through eggs).								
Œnothera Lamarckiana. $x = 7$. van Overeem, 1920	1	9	4	2	2	—	1	1
Œ. biennis. $x = 7$. van Overeem, 1920 . .	41	26	4	—	—	—	—	—
Datura Stramonium. $x = 12$. Blakeslee, 1924 . .	215	381	101	—	—	—	—	—
Solanum Lycopersicum. $x = 12$. Lesley, 1928 .	10	38+	16+	2	—	—	—	—
Zea Mays. $x = 10$. McClintock, 1924 .	—	1	3	1	3	1	—	1
$2x \times 3x$ (*i.e.*, through pollen).								
Œnothera Lamarckiana. $x = 7$	—	15	—	—	—	—	—	
Petunia. $x = 7$. Derman, 1931	39	12	—	—	—	—	—	
Solanum Lycopersicum. $x = 12$. . . .	—	2	—	—	—	—	—	
Zea Mays. $x = 10$ . .	37	27	6	2	—	—	—	

$3x$ ***selfed.*** *Crepis capillaris* ($x = 3$) × *C. tectorum* ($x = 4$). Hollingshead, 1930 *b*. CCT plant (from unreduced egg. $2x = \text{CC} = 6$; $3x = \text{CCT} = 10$; $4x = \text{CCTT} = 14$.

Chromosome number	6	7	8	9	10	11	12	13	14
Random expectation	1	8	28	56	70	56	28	8	1
Progeny . . .	59	12	4	4	12*	3	3	3	1†

* All of the composition CCT ($3x$).
† Composition CCTT, *i.e.*, true $4x$ (*cf.* Table 26).

TABLE 40

Transmission of Extra Chromosomes of Trisomics to their Offspring*

		Through Pollen. Per cent.	Through Eggs. Per cent.
Blakeslee (1921) . .	*Datura* ("Globe") .	3	26
Clausen and Goodspeed, 1924.	*Nicotiana Tabacum* † ("Enlarged," $4x+1$).	3·4	35·4
R. E. Clausen, 1930 .	*Nicotiana Tabacum* ‡ ("Fluted," $4x-1$).	2	*ca.* 60
Frost and Mann, 1924 .	*Matthiola* ("Slender") .	20	nil
Lesley, 1928 . .	*Solanum Lycopersicum.*		
	triplo "A" . .	0	24
	,, "C" . .	10	*ca.* 15
	,, "B" . .	23	27

* 50 per cent. expected: the reduction is chiefly due to elimination of abnormal gametes, but partly also to elimination of abnormal zygotes.
† Pentasomic tetraploid.
‡ Trisomic tetraploid: the high transmission of $2x-1$ eggs is due to frequent loss of the unpaired chromosome at meiosis so that more $2x-1$ eggs than $2x$ are formed. No $4x-2$ seedlings appear.

TABLE 41

Transmission of Extra Fragments to Offspring on Selfing $2x+f$ and $2x+2f$ *Solanum Lycopersicum* (Lesley and Lesley, 1929)

Fragment Type.	Numbers of Offspring.		
	$2x$.	$2x$ + f.	$2x+2f$.
f: "D/2" . . .	19	5	1
f: "C/2" . . .	27	20	4
2*f*: "C/2". . .	18 *	45 *	24

* From gametes not having one fragment owing to irregular separation and loss of unpaired fragments at meiosis (*cf.* Table 17).

TABLE 42

Pollen Abortion in Datura (Blakeslee and Cartledge, 1926).

	x	$2x$	$3x$	$4x$
1923–4	88 per cent.	1·2 per cent.	43·6 per cent.	5·2 per cent.
	$2x$	$2x+1$	$2x+2/2$	$2x-1$
1925	1·5 per cent.	(Primary Trisomics) 2·2–10·2 per cent.	Secondary Trisomics) 3·5–12·5 per cent.	(Monosomic Sectorial) >50 per cent.

Notes.—(i) No monosomics in progeny of haploids, therefore $x-1$ eggs and pollen or $2x-1$ zygotes are non-viable.

(ii) The primary trisomics with the poorest pollen are not those with the poorest growth and lowest frequency of appearance in progeny of triploids. Therefore the disadvantageous effect of the extra chromosome is specific in regard to time of action.

(iii) The pollen abortion is higher in the tetraploid than in the diploid (*cf.* Table 27).

The following table summarises the effect of single-section and single-chromosome differences from the normal on various stages of the life cycle in certain animal and plant species.

TABLE 43

Effects of Abnormal Chromosome Constitution on Viability

I. In *Drosophila melanogaster* (Fig. 14; *cf.* Li, 1927).

Deficiency.	Reduplication.
Gametes ($x-1$). Nullo-X and -Y sperm function (Kuhn, 1929) and probably therefore all other aberrant types. All eggs probably fertilised.	($x+1$). All types of egg and sperm capable of fertilisation.
Zygotes ($2x-1$). (i) Sections: some have no effect. Others are lethal to larva.	($2x+1$). (i) Section: no deleterious effect.
(ii) Haplo-IV: development retarded, not lethal.	(ii) Triplo-IV: viability slightly reduced.
(iii) Haplo-II and III: lethal in egg stage.	(iii) Triplo-III and IV: lethal to egg. Usually lethal to larva (" super-female ").
(iv) Haplo-X: viable male (sterile, on account of failure of pairing with Y).	(iv) Triplo-X: usually lethal to larva or pupa (" super-male ").

Deficiency.	Reduplication.
Zygotes ($2x-2$).	($2x+2$).
(i) Sections: homozygous deficiencies lethal in prelarval stages (including deficiencies in *X* of ♂).	(i) Sections: "P III" lethal to larva.
(ii) Nullo-*IV*: little or no development.	(ii) Tetra-*IV*: lethal to young larva.
(iii) Nullo-*X*: no development (similarly nullo-*II* or *III*).	(iii) Tetra-*X*, *II* or *III*: cannot occur.

II. In various plant species referred to in earlier tables (for deficiencies, *cf.* Monosomics).

Gametes, $x + 1$.
Pollen (i) Fragments: viability probably slightly reduced.
(ii) Whole chromosomes: largely eliminated but to a varying extent according to the chromosome.
(iii) Several chromosomes: all eliminated.
Eggs (i) Fragments }
(ii) Whole chromosomes } Unaffected.

Zygotes.
$2x + 1$ (i) Fragments: viability not clearly lowered; show specialised abnormality.
(ii) Whole chromosomes: viability slightly lowered. Show generalised abnormality.
$2x + 2$ (i) Fragments: accentuation of $2x + 1$ type. Viability lowered.
(ii) Whole chromosomes: accentuation of $2x + 1$ type. Viability greatly lowered.

Records of fertility and elimination showing the differentiation of the chromosomes are supported by a large series of qualitative observations. Thus in *Matthiola* (Frost and Mann, 1924; Frost and M. M. Lesley, 1929), *Crepis* (Navashin, 1926, 1929) and *Zea* (McClintock, 1929 *a*) as well as in the examples already given, a whole series of trisomic phenotypes have been identified corresponding with the different members of the complement which are present in excess. Further, these extra chromosomes are specific in the time of their special action as well as in the kind of effect they produce. For example, the trisomic *Datura* type with the worst pollen at maturity is not the one with the lowest pollen effectiveness in fertilisation. Again, the extent of the disproportion always has a quantitative effect ; the tetrasomic has the corresponding trisomic characters in an exaggerated degree, while the same number of chromosomes in a tetraploid or hexaploid have a reduced effect (*e.g.*, *Avena sativa*, $6x$, Huskins, 1927 ; *Triticum vulgare*, $6x$, Kihara, 1919-24, Huskins, 1928 ; *Primula kewensis*, $4x$, Newton and Pellew, 1929), whence the occurrence of only high polyploid species with variable numbers (*v.* Ch. VIII).

Two principles may be inferred :

(i) The parts of the chromosome complement have specific and different properties ; this is the principle of *differentiation*.

(ii) These parts co-operate in the developmental processes of the organism, so that every integral part of the chromosome complement is necessary for the normal development of every part of the organism ; this is the principle of *co-operation*, which is in a sense an *a posteriori* statement of the *a priori* doctrine of epigenesis.

Now when these two principles are considered in relation to adaptation they give it a new character. The adaptation of an organism (gamete or zygote) must be held to consist in an *adjustment* of the proportions of the differentiated particles (genes) to co-operation with one another in joint reaction to external conditions. This adjustment has been described by Bridges (1922) as *balance*. The " normal " or successful type of gamete or zygote in a species is said to be " balanced " while the types with their constituent elements not so proportioned are said to be " unbalanced."

Consider a chromosome complement consisting of n qualitatively differentiated particles (genes). On Bridges' principle the properties of the organism depend on the proportions, *i.e.*, interactions, of these particles. There are $\frac{n(n-1)}{2}$ such specific interactions. Where one particle is reduplicated n of these interactions are changed ; where half the particles are reduplicated the maximum number of interactions are changed, *i.e.*, $\frac{n^2}{4}$. It follows that the maximum unbalance is attained where half the chromosome complement is reduplicated and the least unbalance where the least portion is reduplicated.

This rule applies to *Drosophila*, where the only viable autosome trisomics are the triplo-IV, and to *Solanum Lycopersicum*, where the $2x$, $2x+f$, $2x+2f$, $2x+1$ and $2x+2$ represent a descending series in relation to growth rate (Lesley and Lesley, 1929). It applies to all observed progenies of triploids, which show greater elimination of $2x+2$ and $2x+3$ forms than of $2x+1$. It applies to the size of unbalanced pollen grains in *Tradescantia* (D., 1929 *c*). The rule also means that the smaller the number of particles affected the more specific will be the effect on the organism. It is found that extra fragments have a more restricted effect in *Solanum*. Also it may be noted that as many as three homologous fragments are found reduplicated in apparently normal forms of *Fritillaria*, where each fragment is equivalent to 1/200th part of the whole set.

It also follows that where the change in proportion is from 1 : 1 to 2 : 1 the effect should be more drastic than where the change is from 2 : 1 to 3 : 2. Thus tetrasomics (whether of fragments or whole chromosomes) are more markedly abnormal (in viability as in other respects) than the corresponding trisomics in *Datura*, *Solanum* and *Matthiola*.

The principle of balance operates co-extensively with qualitative differentiation. Moreover, variation in the degree of differentiation between chromosomes is probably due to their being sometimes similarly differentiated—in plants, no doubt, owing to a remote polyploid ancestry. *Hyacinthus orientalis*, for example, shows reduced unbalance in trisomics and hence reduced sterility in triploids. It is possibly in its remote origin a tetraploid (*v.* Ch. VIII and p. 243).

This contrast between balance and unbalance conveys the impression of something denigratory about unbalance, and, as we have seen, unbalanced forms are usually maladjusted in proportion to the amount and frequency of the particles concerned. But particular exceptions show that this rule is no absolute one. Certain kinds of unbalance are hardly inferior to the normal condition. The difference between balance and unbalance must therefore be expressed in relative terms thus: The balanced combination of genes has been exposed to natural selection. The unbalanced combination has not; it is at random, and since the possibilities of random combination are vast (most organisms probably having some thousands of differentiated genes) and the number of successful combinations possible in any one environment are few, the chances of a new unbalanced type being as successful as the normal are remote.

These arguments may be inverted, and we then see natural selection from a different point of view, which is not without value. We may say that natural selection consists in the elimination of unbalanced forms from the body of proportion-variants and gene-variants in a species.

(*c*) Secondary Balance. From these considerations it follows that the possibility is always open of variation occurring by a change in proportion, either by reduplication of segments of chromosomes or of whole chromosomes. If such a new proportion were successful it would yield a new *secondary balance* having a different phenotypic expression from the primary, ancestral, type. Evidence of this probably universal type of variation is only beginning to appear, for the reason that the necessary inferences are elaborate ones.

Where the change of balance is concerned with whole chromosomes its occurrence seems to be confined to polyploids. Thus the 18-series arises in *Dahlia* secondary to the 8-series and the 17-series in the Rosaceæ secondary to the 7-series (*v*. Ch. VIII). The primary balance in the 17-series is shown by the critical test of triploid progenies. Thus in the progeny of triploid-diploid crosses the following distribution of chromosome number types is found in *Pyrus Malus* (Moffett, 1931):—

Chromosomes in excess of 34:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Nos. of seedlings	–	–	1	4	2	5	10	2	4	1	1	1	1	—	—	—	—

This distribution is different from that characteristically found in simple triploids already discussed where intermediate numbers are eliminated. The favouring of seedlings with seven extra chromosomes suggests that these are the seven that make up the primary set whose existence is inferred on other grounds.

In *Nicotiana* ($x = 12$) also the progeny of triploids having 12 bivalents and 12 univalents do not show the sharp elimination found in simple triploids. The middle number is favoured, as the following results show :—

1. Distribution of the extra 12 chromosomes in the triploid *Nicotiana sylvestris* ($n = 12$) × *N. Tabacum* ($n = 24$) at meiosis, showing randomness, and in the progeny of the back-cross to *N. sylvestris* ♂, showing some elimination. (The total numbers of observations are given in brackets.)

No. of extra chromosomes .	0	1	3	3	4	5	6	7	8	9	10	11	12
1. Second metaphases (207)	0	0	4	11	18	41	66	32	26	6	2	1	0
2. Progeny (17) $2n = 24+$	1	5	3	1	1	1	1	1	1	1	–	–	2

2. Distribution of extra 12 chromosomes in the triploid *Nicotiana paniculata* ($n = 12$) × *N. rustica* ($n = 24$) in the back-crosses to the parental species (Lammerts, 1929, 1931).

No. of extra chromosomes	0	1	2	3	4	5	6	7	8	9	10	11	12	24*
1. $3x$ × *rustica* ♂ (78) $2n = 36+$	–	–	–	3	8	12	12	–	7	1	–	–	–	35
2. $3x$ × *paniculata* ♂ (117) $2n = 24+$	–	5	3	4	17	16	24	6	10	4	–	–	–	28
3. *rustica* × $3x$ ♂ (44) $2n = 36+$	–	–	–	–	–	–	4	3	2	2	–	3	30†	–

* Through failure of reduction.

† Gametic selection on male side is determined by relationship to female parent as in *Œnothera*

These results may be explained as due to a lack of differentiation in the chromosomes or to the set of twelve being derived from an earlier set of six by polyploidy. The latter view is the more probable and is favoured by some evidence of secondary pairing in *Nicotiana* and by general statistical considerations (*v.* Ch. VIII). Thus *Nicotiana* with an apparent basic number of 12 may be said to have a primary basic number of 6 from which the secondary basic number of 12 (of unaltered phenotypic expression) is in process of developing—without, however, any change in balance in the whole set.

The second kind of evidence of change of balance in evolution consists in the occurrence of intra-haploid homology, *i.e.*, the reduplication of materials (genes) within the haploid set. This may be inferred from both genetical and cytological observations, which indicate that pairing occurs exceptionally between chromosomes in the same haploid set in the absence of competition, as follows. (These observations will be better understood after a study of the later chapters referred to) :—

(*a*) In haploids: *Œnothera*, Emerson, 1930; Catcheside, 1932. *Zea Mays* (polymitotic strain), Beadle, 1931. The pairing is exceptional and occurs as a rule only between two chromosomes in the set (Ch. XIII).

(*b*) In diploid interchange heterozygotes: *Œnothera*, D., 1931 *c* (Ch. XIV).

(*c*) In trisomic diploids: *Œnothera*, Håkansson, 1930 *b*, interstitial chiasmata frequently occur whose terminalisation can only have been arrested by a change of homology (*v*. Ch. XII); they indicate pairing of sections intercalated in non-homologous chromosomes.

It may be thought remarkable that pairing (and crossing-over) should occur between parts of chromosomes in the haploid, although these parts never seem to pair in the diploid, especially since in *Œnothera* this pairing is often terminal, proving that the ends of some of the different members of the haploid set are homologous. How does this agree with the notion that the parts of the chromosomes are qualitatively differentiated? A comparison with the observations of differential affinity in polyploids shows the explanation (Ch. VII). It is known that chromosomes which rarely or never pair, in an allotetraploid, may pair regularly in its diploid hybrid parent or its parthenogenetic diploid progeny. Thus it is not surprising that chromosomes which never pair in the diploid should occasionally pair in its parthenogenetic haploid progeny for the same reason. Two "non-homologous" chromosomes of the haploid set may consist of a series of particles (or genes) *abcdefghkl* . . . and *amnopqrs* . . . In the presence of identical mates, *i.e.*, with the same linear sequence of particles, the *a* particles of different chromosomes will never pair. In the haploid they will very often pair at pachytene and occasionally form a chiasma which will preserve their pairing at metaphase.

Where such corresponding particles are intercalary, crossing-over at this chiasma will mean the interchange of non-homologous segments (*v.* Ch. X). Hence the progeny will show new combinations of genes ; it will yield mutant types. These have been found in the expected circumstances, both as regards the form of the chromosomes and the genetical properties of the plant, as follows :—

A. NEW CHROMOSOME FORMS.

(i) *Solanum Lycopersicum* (Lesley and Lesley, 1929). $2x+1+1$ plants had progeny with fragments, $2x+1$ plants had not. The fragments are therefore probably due to crossing-over between the two extra chromosomes at non-corresponding positions.

(ii) *Nicotiana Tabacum* (R. E. Clausen, 1931). $4x-1$ plants had twenty-three pairs and one unpaired chromosome. They mutated in the unpaired chromosome to the characters " coral " and " mammoth." In derivatives having the complete forty-eight chromosomes but heterozygous for these new characters the affected chromosome failed to pair. This is characteristic of a chromosome differing structurally from its homologue. Moreover, crossing-over did not take place between the two new factors. This is also characteristic of structural hybridity. Finally, a third mutant " flaking " arose through fragmentation of the same chromosome. There can be no doubt therefore that a series of structural changes occurred in the unpaired chromosome, and these can be explained as the result of this chromosome pairing and crossing over " illegitimately " with homologous segments of non-homologous chromosomes.

(iii) The progeny of certain triploid *Crepis* hybrids considered later, with new chromosome types, may be due to this illegitimate crossing-over.

(iv) *Matthiola incana* (Frost, 1927). A particular trisomic " crenate " gives a particular fragment determining the " slender " character with a specially high frequency. This can best be accounted for by crossing-over between translocated segments.

B. NEW GENETIC TYPES.

New mutations occur with high frequency in the progeny of trisomic and of haploid *Œnothera* (Davis and Kulkarni, 1930; Stomps, 1931).

All these observations are in agreement with the theory of mutation, outlined elsewhere (Ch. XIV), which demands that in *Œnothera*, as in other organisms, small sections should be homologous in different parts of the same haploid complement and of different complements. This would mean that there had been a considerable amount of reshuffling of small pieces of chromosome in the history of the species, the primary change being translocation, and the secondary change, reduplication.

Since every gene or series of genes must be supposed to have once been singly represented in any chromosome complement, reduplication of genes means change of proportion, which if successful becomes secondary balance. All chromosome complements are probably secondary in this sense, for such change is perhaps the most readily available source of successful variation in all organisms. Its further analysis is therefore a most pressing problem.

If single genes or blocks of genes are freely liable to reduplication within the haploid set, as these observations suggest, we must suppose that characteristic haploid sets will probably contain a proportion, perhaps a majority, of their genes represented two, three or more times. The gametic set of an autotetraploid will have all its genes present an even number of times and odd numbers will be restored to it by mutation, until it reaches an allopolyploid condition which will not be distinguishable from that of a diploid.

Haldane (1932 *a*) has suggested that chromatin-diminution requires localisation of certain genes; this effect might be produced by the extensive reduplication of all or most of the genes.

This conception makes the occurrence of forms with different degrees of qualitative differentiation as between different chromosomes intelligible. If one species has very little reduplication, all its chromosomes must be differentiated in the highest degree compatible with random assortment of the genes among the chromosomes. If another form has a great deal of reduplication with most of its genes represented six or a dozen times it will have a very low differentiation with the same random assortment. Thus it is not necessary to assume that organisms with low differentiation have individual genes of any special kind but merely that they are reduplicated more frequently either at one stroke with polyploidy, or segment by segment with diploidy and structural change.

3. THE GENE IN RELATION TO MUTATION AND BALANCE

We may now pause to consider for a moment our knowledge of the physiological properties of the hereditary material. This knowledge is derived from three series of observations. The first, a comparison of organisms with different proportions of different chromosomes or parts of chromosomes, shows that the hereditary material is qualitatively differentiated. The second, based on the mode of inheritance of differences between organisms, shows that the properties of change in different parts of the hereditary material (which are linearly arranged) are apparently specific to those parts. We may therefore equally infer by this indirect means that the hereditary material is differentiated into qualitatively distinct particles. Finally, the observation of the specific pairing properties of the constituent particles making up the chromosomes (especially conclusive at zygotene in polyploids) requires the assumption of a linear differentiation of the chromosomes into particles having specifically different properties. Thus from three directions we are forced to the conclusion that the hereditary material is made up of specific particles which behave as units. To these particles, for theoretical purposes, we apply Johannsen's term " gene."

The notion of the " gene " derived in this way is exact and universally applicable, but the very fact that the notion is inferred from three different kinds of observation leads to inconsistency as soon as it is used in describing the conclusions from any one of these different sources—a confusion which was responsible for the misgivings voiced by Johannsen in 1923. Furthermore, the inference of the gene is made with various degrees of directness. Qualitative differentiation is shown by unbalance, in which large groups of genes are probably concerned. Specificity in pairing properties is usually inferred from observation of chromosome pairing at metaphase of meiosis in hybrids, and this is a remote derivative of the conditions which determined it at pachytene. Specific variation is shown by the observation of the effects of differences in the genes, and the word gene is sometimes used loosely to mean the differences themselves.

In order to describe these different kinds of observations consistently in terms of "genes," we must try to infer their relationship accurately. This seems to be possible by the following steps :—

(i) Particular genes must be supposed to be of a constant chemical type determined by a typical molecular constitution.

(ii) The properties of the genotype can be changed, or differences can arise, through changes : (*a*) in the quantity of any gene present (as shown by changes in the quantitative effect of a gene such as "Bar," and perhaps the sex genes inferred by Goldschmidt) and by the occurrence of structural changes such as deficiency and reduplication ; and (*b*) in the chemical properties of a gene : that this type of change occurs, as distinct from the first, follows directly from the principle of specificity. The different genes making up one genotype and all the genes making up two entirely different genotypes must be qualitatively, and not merely quantitatively, distinct. Differentiation both between the genotypes of different species and within the genotype of any one species must have arisen from qualitative, *i.e.*, intra-genic, change. Differentiation and variation are symptoms of the same phenomenon.

(iii) Since the genes show qualitative differences the notion that mutation, and hence evolution, is determined by either hybridisation or structural change is inadequate. These can only effect change when the genes are already differentiated ; they cannot themselves determine this differentiation. Sax's suggestion (1931 *b*) that unequal crossing-over determines mutation, for these reasons alone (apart from the uneven distribution of genes on the crossing-over map and other genetic evidence, *v.* Sturtevant, 1925), falls to the ground.

Parenthetically it may be noted that the distinction between two different types of gene change according to their *cause* (qualitative and intra-genic or quantitative and inter-genic) has no necessary relation to a classification according to their *effect* (lethal,inactivating and so on).

(iv) On the distinction of cause the relationship of the gene to the three kinds of evidence for its existence may be defined. Qualitative differentiation which gives the phenomenon of balance arises from intra-genic (*i.e.*, intra-molecular or chemical) change, which is of precisely the same kind as one of the types of gene-difference observed. To give a practical example, the balance between *X*-chromosomes and autosomes in *Drosophila* which determines sex, must have arisen by intra-genic change probably in both the *X* chromosome and in the autosomes. And therefore the phenomenon is indirect evidence of just the kinds of difference that distinguish the *X* chromosomes or the autosomes of different species, races and mutants, as shown by Bridges and Goldschmidt (*v.* Ch. XIV).

(v) The fact that two different kinds of change may occur to any particular gene means that the method of differences between allelomorphs provides an uncertain indication of the properties of the gene when the two kinds cannot be distinguished.

(vi) Since we assume that all distinctions between genes, both within and between species, arise from the same kind of intra-genic change, it follows that this kind of change must inhibit pairing of the differing genes. Thus pairing of genes may be prevented at pachytene by either of the two changes which are ordinarily described genetically: intra-genic change will prevent pairing of two genes, quantitative change will prevent pairing of a larger or smaller group of genes according to the number affected (which may amount to the whole chromosome). Therefore quantitative or structural change will be a vastly more potent means of preventing pairing, and the failure of pairing in hybrids may therefore be taken as an indication of the part structural dissimilarity between corresponding chromosomes has played in the differentiation of their parents. Further, it follows that allelomorphism is essentially a function of position in the chromosome rather than of chemical relationship.

4. SEGREGATION

So far we have considered the physiological properties of chromosomes in relation to heredity. We must now consider their mechanical properties.

The pairing and separation of the chromosomes is clearly parallel to genetic segregation, as pointed out by Sutton in 1902. The assumption that the one determined the other made it possible to predict haploid or gametic segregation, which has since been abundantly demonstrated genetically. Special cytological observations have since made it possible to verify converse predictions in various ways, as follows:—

1. Carothers (1921) showed that when grasshoppers (*Circotettix*) with unequal pairs of chromosomes at meiosis were bred with related forms homozygous for chromosome structure, they produced offspring half with one type of chromosome and half with its mate. This was a combined demonstration of (*a*) chromosome permanence and heredity, (*b*) meiotic reduction and mendelian segregation, and (*c*) fertilisation and mendelian recombination.

2. Federley (1913, 1930) showed that *Pygæra* hybrids having no pairing and no reduction of chromosome number at meiosis (*v.* Ch. XIII) showed no segregation of parental characters.

3. Similarly in parthenogenetic organisms where pairing fails there is no segregation (*cf.* Ch. XV).

4. In all allotetraploids formed by doubling of the chromosome number in a hybrid there is a suppression of segregation. This suppression is partial or almost complete according as pairing is partially or completely suppressed between chromosomes of opposite parental species. Thus in *Raphanus-Brassica*, where no segregation occurs, no pairing of *Raphanus* and *Brassica* chromosomes occurs—simple bivalents are always formed in the tetraploid (and no bivalents are formed in the diploid). In *Primula kewensis*, on the other hand, segregation does occur in the tetraploid; quadrivalents are formed.

5. Where four, six or more chromosomes are associated in a ring in a diploid, each of these chromosomes must have a specifically different combination of materials from any of the others, and only two types of viable gametes should be produced—the opposite types

arising from separation of each chromosome in the ring from the other two with which it is "paired" at opposite ends. This is verified both by genetical and by cytological tests of the progeny. It is found that two such gametic types are produced by wild species with chromosome rings (*v.* Ch. XIV), and these differ genetically. Similarly the inheritance of the pairing properties of their chromosomes agrees with prediction. Each form with rings produces two kinds of gametes which give specific and different kinds of pairing or ring-formation with other kinds of gametes (*v.* Chs. VI and XIV).

6. From the study of the products of segregation of single mother-cells in the haploid phase in Bryophyta (*Sphærocarpos* and *Funaria*), and in Basidiomycetes, it has been shown that segregation in regard to a particular character may take place either entirely at the first division, entirely at the second division or partly at the first and partly at the second division (v. Wettstein, 1924; Allen, 1924; *cf.* D., 1931 *c*). This agrees with the methods of division of unequal bivalents (Ch. X).

7. In every instance in which the sexes are visibly different in their chromosome complements (as they are in most animals and many plants) the segregation of dissimilar chromosomes can be seen in the sex heterozygotes at meiosis, and in some the whole history can be traced, from the random segregation to the sexual differentiation of the dissimilar products of this segregation (Ch. XIV). In the higher plants the sexual differentiation does not express itself in external form until long after meiosis. This is true of the sporozoan *Aggregata* and has led Dobell (1925) to believe that the differentiated gametes might be derived from the same haploid cell and so the differentiation might not spring from segregation at meiosis. Further study (Naville, 1931) and closer reasoning (Belar, 1926; M. Robertson, 1929) have shown that this assumption is unjustified.

8. Where segregation is occurring in factors carried by chromosomes represented more than twice (in polysomic and autopolyploid plants) the proportions of offspring bearing the opposite characters occur, not in the simple mendelian proportions but in the more complex proportions to be predicted from the random assortment

of the larger number of chromosomes concerned (*cf.* Haldane, 1931 *a*, Crane and D., 1932, and Ch. X).

The parallelism between chromosome reduction and genetic segregation is therefore complete so far as whole chromosomes are concerned. The specific properties of segregation shown by parts of the same chromosome in the phenomenon of linkage will be considered in the next chapter.

CHAPTER X

THE CHROMOSOMES IN HEREDITY. PART II
CROSSING-OVER

Genetic Crossing-Over—Cytological Theories—Chiasmatypy—Proof of Crossing-Over—of Whether, and When, it Occurs—Parallel Inferences—How Crossing-Over Occurs.

"Die bei der Reifung der Geschlechtszellen eintretende Verklebung vorhergetrennter Chromosomen bezweckt einer Substanzaustausch derselben."

RÜCKERT, 1892.

"Dans tout le règne animal et dans le règne végétal on voit apparaître la tétraspore. Cette formation a donc une importance capitale. S'il se produit là quatre spores et pas deux, c'est qu'elles doivent avoir chacune quelque chose de particulier."

JANSSENS, 1909.

1. THE THEORY OF CROSSING-OVER

(i) **Introduction.** There is no longer any question, either on cytological or on genetic evidence, that crossing-over or exchange of segments may take place between paired homologous chromosomes at meiosis. But the precise cytological conditions of crossing-over are a matter of debate. They are of profound importance in many different ways: (i) A knowledge of the conditions of crossing-over is necessary for the understanding of the mechanical properties of the chromosomes. (ii) Crossing-over must be understood in its relation to structures observed cytologically, on account of its importance (*a*) as a means of investigating the linear arrangement of the genes, (*b*) as the possible cause of secondary and even primary structural changes at meiosis, and especially of mutation in complex heterozygotes (Ch. XIV). The first of these depends on the change of combination of unit mendelian differences, the second on the change of combination of cytologically observable differences. (iii) Certain properties of the chromosomes in crossing-over are likely to be revealed more accurately cytologically than genetically.

(iv) A precise notion of the cytological basis of crossing-over is necessary in examining the probable origin of sex chromosomes and of parthenogenesis, and in other evolutionary questions (Ch. XVI).

(ii) **The Genetic Theory.** In all organisms in which the inheritance of a large number of mendelian factor-differences has been studied, certain of these have been found to be "linked," *i.e.*, when individuals differing in two such factors are crossed, the proportion of new combinations in the second generation is lower, and of old combinations higher, than would be expected from free assortment (according to Mendel's second law). The general conditions of this linkage are similar in most structurally homozygous diploids that have been studied, *e.g.*, in *Drosophila* species, *Zea Mays*, *Primula sinensis*, *Pisum sativum*, etc., and observations of exceptional linkage in *Lebistes*, *Apotettix*, *Cepea* and *Funaria* are becoming intelligible in these terms since the very great irregularity in the distribution of the genes in the *Drosophila* chromosomes was discovered.

Linking can be accounted for, as Morgan showed in 1911, by supposing that the factors concerned are located at certain fixed distances from one another in the chromosome, and that the recombinations of factors that occur are due to "crossing-over" or an exchange of homologous segments between them. Thus, if the factors are at opposite ends of chromosomes : *ABCDE* and *abcde*, crossing-over might give *ABCde* and *abcDE*. Crossing-over should then be not rarer between *A* and *C* than between *A* and *B*, owing to its being conditioned by distance, and this can be verified where two factors are linked with a third. The amount of crossing-over between the two should, when small, approximate to either the sum or the difference between the amounts of their crossing-over with the third. This is always the case in organisms with simple pairing of chromosomes. But the exact relation is not a simple one as might be supposed, *i.e.*, the resultant crossing-over is not equal to the sum of the two smaller proportions *minus* twice their product (to allow for double crossing-over which would cancel itself out), but *minus* something less than this. It follows that double crossing-over between factors fairly close to one another is not so frequent as randomness requires ; the occurrence of one cross-over may therefore be said to "interfere" with the occurrence of another in its neighbourhood, and the property is known as "interference."

These principles must be understood in order to follow the cytological evidence. The conditions of crossing-over will be examined in detail at a later stage in relation to this evidence.

(iii) **The Cytological Theory.** The observation that the chromosomes paired at diplotene came together at various points along their length—points which we now recognise as chiasmata—suggested to Rückert in 1892 that the chromosomes exchanged material at these points. The view was ignored in the following years, being naturally overshadowed by the idea of permanence in the structure of the chromosomes. The four chromatids of the bivalent were usually supposed to be derived without change, two from one parental chromosome and two from its mate. The question then was merely whether the two chromatids which passed to the pole together at the first division were derived from the same parental chromosome or from the two partners. In the first case the first division would be "reductional" in respect of differences between the partners, in the second case it would be "equational." A third point of view, that the chromosomes fused and lost their identity at meiosis, need not now be considered.

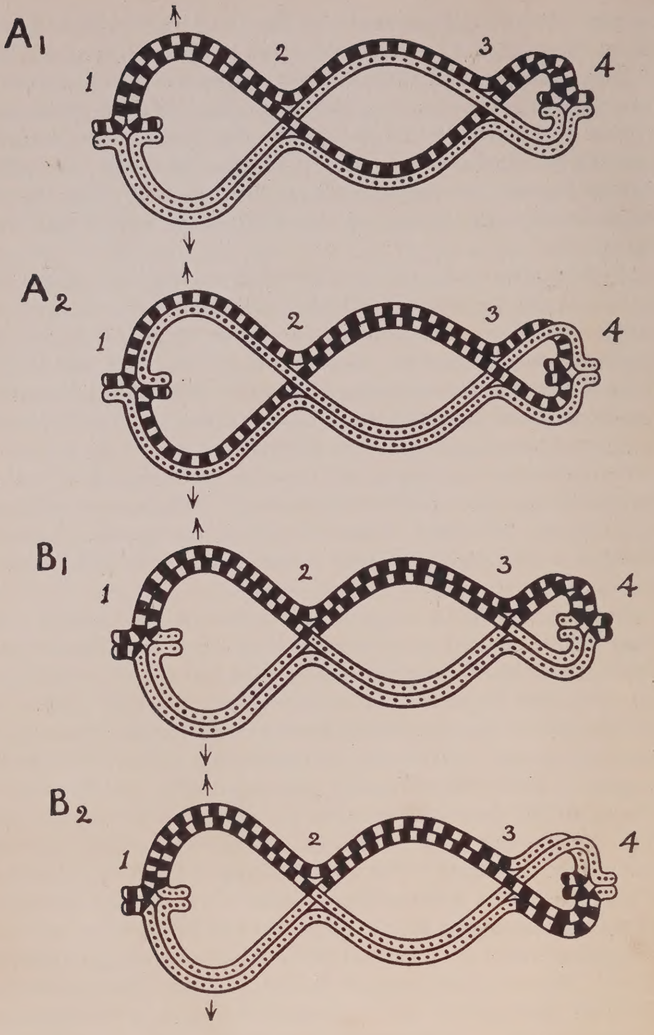
The controversy was confused owing to a lack of distinction between numerical reduction and qualitative reduction. We now know that reduction in number does not occur at either division, but simply through the two divisions following one another so rapidly that no division of chromosomes takes place in the interphase between them. We also know that reduction in quality, *i.e.*, the separation of unlike chromosomes, occurs both at the first and at the second division (at least so far as different bivalents are concerned) under conditions which will later be defined.

While this dispute was still undecided, Janssens (1909) put forward the objection that the formation of four spores or gametes at meiosis, the occurrence of two divisions, of pachytene pairing, and of the diplotene looping, would all lack *purpose* if reduction was achieved at a single division and without crossing-over. These arguments are of great value taken metaphorically; but Janssens also pointed out that without the assumption of an exchange of segments at the chiasmata the exchange of partner lacked any causal explanation. He pointed out that there was free association of larger number of factors in some organisms than there were chromosome pairs; this was genetic evidence of such exchanges. Applied to *Drosophila* this theory was the basis of the successful study of the linear arrangement of genes from the occurrence of crossing-over or exchange of segment between homologous chromosomes. The results of this study have been considered above.

There was, however, no unequivocal direct evidence either for or against the hypothesis, and later Wenrich (1916) was able to describe the development of paired chromosomes in *Phrynotettix* on the assumption that no crossing-over had occurred and that a chiasma was due to the meeting of loops separating the chromatids equationally and reductionally (*cf.* also Granata, 1911). This will be referred to as the " classical " theory.

Two chromosomes went into pachytene association: four chromatids emerged at the diplotene stage. Whether an exchange had occurred no direct evidence could or can reveal. Indirect evidence was available. It was neglected and will be considered here for the first time.

Janssens later (1924) supported his " chiasmatype " theory with observations on two grasshoppers, *Mecostethus* and *Stenobothrus*. These give us the most exact and detailed account of meiosis that has ever been prepared. We can now see, however, that it is defective in two respects. First, Janssens did not record statistically the numbers and distributions of chiasmata at different stages of prophase. He therefore thought that chiasmata might be reduced in number in *Mecostethus* between diplotene and metaphase, and that this was due to breakage and reunion of chromatids which resolved the chiasmata. But on the analogy of *Fritillaria Meleagris* it is probable that two or three chiasmata very close together at metaphase may appear as one. Janssens also thought that terminal associations result from contact without crossing-over, and not, as is now believed, from terminalisation of interstitial chiasmata. Secondly, Janssens did not recognise that all points at which four chromatids come together at diplotene are points at which the pairs



A1
A2
B1
B2

FIG. 68.—Diagram to show the distinction between different genetical interpretations of the same diplotene bivalent. This bivalent has four chiasmata which have different structural relationships with one another (apart from any genetical assumptions). Thus the second does not restore the association broken by the first; they are "non-compensating"; the second and third, the third and fourth, on the other hand, are compensating (*v.* Fig. 29, B and C). At anaphase there will be interlocking of chromatids in the loop between the second and third chiasmata (*v.* Fig. 29, C). A_1 and A_2, alternative interpretions on the classical theory, A_1, Wenrich, 1916, *v.* Granata, 1911; A_2, D., 1929 *b* (1 is an "equational" chiasma, the rest are "reductional"). B_1 and B_2 alternative interpretions on Janssens' hypothesis of "partial chiasmatypy" as simplified by Belling, 1928*c*, and Darlington, 1930 *b*. In *B*, non-compensating chiasmata (1 and 2) arise from crossing-over of one chromatid at both chiasmata and two different chromatids once at each chiasma ("diagonal crossing-over"). Compensating chiasmata arise either from both affected chromatids, being the same (2 and 3 in B_1, and 3 and 4 in B_2, "reciprocal crossing-over"), or from both being different (3 and 4 in B_1, 2 and 3 in B_2, two "single cross-overs").

of chromatids exchange partner. He considered that they were sometimes due to interlocking of chromatids, following crossing-over between all four, and sometimes merely points of contact or "fusion" without a chiasma. Janssens defined a chiasma in the following terms (translation) :—

"The word chiasma may be taken in the general sense of two threads which cross one another in a Cross of St. Andrew."

It should be noted that the same exchange of partners which appears as a St. Andrew's cross (2 and 3 in Fig. 68) will appear as a Greek cross (1 and 4 in Fig. 68) from another point of view. The word *chiasma* is therefore in the present work defined as *an exchange of partner amongst four chromatids associated in pairs.*

Janssens had a notion of the structure and history of bivalent chromosomes less clearly defined than is possible to-day. This he combined with a clearly defined notion of the genetic relationship of the chromatids which were associated in the bivalent. He assumed, in contrast with Granata and Wenrich, that *sister chromatids are held together, partner chromatids repelled, at diplotene* (Fig. 68, B_1 and B_2). All loops in this case are said to be reductional.

The result of this combination was a complex view of the causes of crossing-over. He assumed that it might happen in any of the following four ways :—

(i) *Between two chromosomes before division into four chromatids, at zygotene or pachytene, determining an interlocking or fusion at diplotene.* Interlockings and fusions of chromatids have not been observed. All such appearances are due to true chiasmata, so that this hypothesis of "total chiasmatypy" can be disregarded (Fig. 73).

(ii) *Between two of the four chromatids after division of the chromosomes at pachytene, determining an exchange of partner.* There is no evidence against this assumption of "partial chiasmatypy," and it will be considered later in detail.

(iii) *Between two of the chromatids at a chiasma at diplotene through breakage and reunion in such a way as to leave no exchange.* Since the exchange itself resulted from crossing-over between two, the new cross-over might rectify the first or produce a second. This assumption will be considered later.

(iv) *Between two chromatids of one chromosome at interphase.*

The chromatids are less closely associated at this stage than in a somatic mitosis which is otherwise similar, so that this assumption is out of the question.

Objections to these assumptions taken as a whole, and particularly the occurrence of great differences of crossing-over frequency between the sexes in most organisms, such as had not been paralleled by observations of differences in chiasma frequency, led to hypotheses supposing that crossing-over was not the *obligatory cause* of chiasma formation (as in (ii) above), but a *facultative consequence* (as in (iii) or otherwise). Such hypotheses are of even less working value than that of Janssens, since they are necessarily even more difficult to disprove. They assume that chiasmata arise through opening of equational and reductional loops, and that crossing-over occurs as follows :—

(v) Between two chromatids at a chiasma as the chromosomes separate at the beginning of anaphase, in such a way that the chromatids in the arms distal to the chiasma do not need to pull apart (Chodat, 1926 ; Maeda, 1930 *b*). The assumption of breakage and reunion at this moment is contrary to all the most detailed observations of anaphase (*v.* Figs. 24, 29 and 36). The hypothesis cannot therefore be entertained.

(vi) Between two chromatids through breakage and reunion after diplotene in such a way as to resolve the chiasma (D., 1929 *b*). This is analogous to Janssens' third assumption, except that chiasmata were supposed to have arisen without crossing-over either through the meeting of reductional and equational loops or through the meeting of two equational loops. These latter chiasmata (Fig. 68, A_1) were called "equational" chiasmata, since their breakage would not lead to genetically visible crossing-over, and it was supposed that the difference in crossing-over between the sexes might be accounted for by the chiasmata being largely equational in one sex but not in the other. The discovery of the reduction in the number of chiasmata during terminalisation has led to the revival of the hypothesis of breakage after diplotene (Sax, 1930, 1931 *a*), but it must be discarded, along with Janssens' assumption, for five chief reasons :—

(*a*) Conditions of crossing-over are similar in *Primula*, *Pisum* and *Lathyrus*, but terminalisation, with reduction in number of chiasmata, is complete in *Primula* while it is negligible in *Lathyrus* and slight in *Pisum* (*v.* Table 46).

(*b*) Where terminalisation of chiasmata is absolutely arrested by change of homology (*v.* Ch. XII) no breakage occurs. It cannot therefore be supposed to occur in the absence of any such impediment.

(*c*) Exact statistical comparison of succeeding stages of prophase fails to show evidence of breakage (*cf.* Ch. XII).

(*d*) The frequency of pairing of fragment chromosomes, of odd chromosomes in triploids, and the frequency of different types of quadrivalent configurations in autotetraploids can be predicted on the assumption of direct relationship between terminal and earlier interstitial chiasmata, and not on the assumption that breakage ever occurs (Ch. XIII).

(*e*) Interlocking of the types expected on this hypothesis has never been found (*v. infra*).

Janssens made the mistake of failing to separate his hypotheses, and he also failed to distinguish between the relative weight of evidence of different kinds in its favour. His critics (Seiler, 1925; McClung, 1927 *b*) have followed his example. They have examined them and discussed them as a unit. They have assumed, as Janssens seems to have assumed, that if crossing-over occurred "direct proof" of it should be available. They have shown that the weaker parts of the evidence are not a proof on any justified assumption. Our task therefore is to dissect the hypotheses, reject those that are impossible and examine the evidence for those that remain, separating them into classes according to the assumptions which have to be made in applying them to the problem. These assumptions must all be purely cytological; otherwise they merely beg the question.

With regard to the hypotheses: for the reasons given above it must be concluded that Janssens' second assumption, that sister chromatids are associated on both sides of any chiasma and that therefore *crossing-over takes place between two chromatids of different chromosomes at the chiasma before it is formed*, is the only one which stands the test of observation (Belling, 1927 *a*, 1928 *c*; D., 1930 *b*).

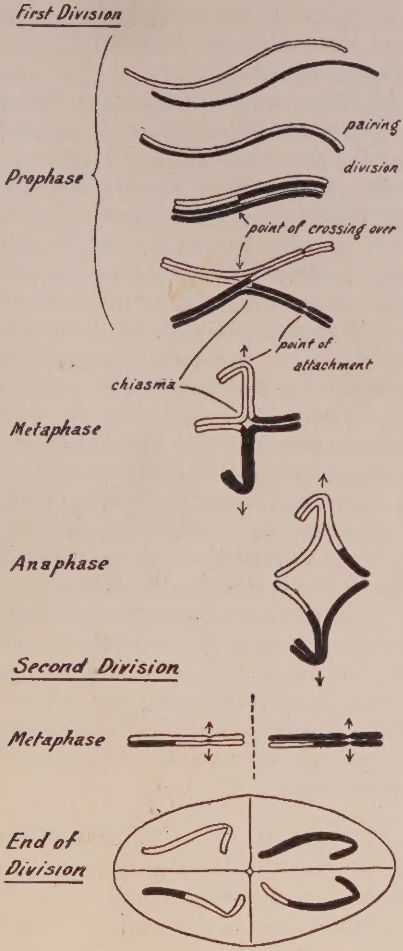

First Division
Prophase
pairing
division
point of crossing over
point of attachment
chiasma
Metaphase
Anaphase
Second Division
Metaphase
End of Division

FIG. 69.—Diagram showing the history of two homologous chromosomes at meiosis according to the chiasmatype hypothesis. *Note.*—The four daughter nuclei all contain chromosomes of different origin owing to crossing-over.

This will be referred to in future as the "chiasmatype hypothesis" (*sensu stricto*) as opposed to the "chiasmatype theory" with its more complex assumptions.*

Combined with the assumption that all apparent points of contact between four chromatids at diplotene are exchanges of partner between them, *i.e.*, chiasmata (D., 1929, *b* and *c*) the re-defined hypothesis enables us to examine bivalent formation in all plants and animals critically for decisive evidence. This evidence can be classified logically according to what it proves in relation to crossing-over and on what assumptions the proof is valid. Thus one kind of evidence shows *whether* an exchange of segments occurs in hybrids when crossing-over is observed, a second shows *when* and *where* it occurs, a third shows *how* it occurs. These proofs are proofs of increasing specificity, for the second implies and includes the first, and the third includes both. They are also proofs resting on increasingly large assumptions (which will be stated) and therefore involving increasing doubts. For both these reasons they must be considered in the order given. We must first find out whether crossing-over can be proved cytologically. We must then examine when and where it occurs, and last of all we may attempt to find out by cytological tests how it occurs (*cf.* p. 343).

The second section deals with proofs that are valid on assumptions that have been justified by evidence elsewhere. The third section deals with potential proofs that are not valid in this sense: they constitute merely "indicational evidence." Some of the proofs are answers to the questions of whether crossing-over occurs on one set of assumptions, and to the question of when it occurs, on other and greater assumptions.

2. CYTOLOGICAL PROOF OF CROSSING-OVER

(i) Proof of Whether Crossing-over Occurs. When a numerical change occurs in the chromosome complement, such as triploidy, it inevitably entails *secondary* changes through the abnormal behaviour of the new numerical hybrid at meiosis. The new form gives rise to trisomic and tetrasomic offspring. In the same way structural changes may be distinguished according to whether they are of a primary character, arising without any relation to segregation at meiosis, or of a secondary character, arising from this segregation in the primarily changed form. Thus, clearly, deficiency and reduplication are secondary results of either fragmentation or translocation, owing to the random segregation of the changed and unchanged chromosomes at meiosis.

---

* It should be noted that the chiasmatype theory explains the *cause* of chiasma-formation and has immediate genetic implications. The chiasma theory of pairing (Chs. IV, VI, XI) explains the consequence of chiasma formation—the maintenance of prophase pairing to metaphase—and has no such implications. The two are unrelated.

But if crossing-over occurs between the parts of chromosomes it should give rise to a special category of secondary structural changes. Where two chromosomes dissimilar at both ends cross over in the middle, two chromosomes involving new combinations of parts will appear. Such changes therefore will be *prima facie* evidence of crossing-over. If then they occur regularly or with special frequency particularly in organisms known to be structural hybrids or having unpaired chromosomes of one set (as in a haploid or triploid) with possibly homologous parts, the conclusion that crossing-over has taken place is scarcely avoidable. Finally, when the occurrence of crossing-over assumed in particular individuals on cytological grounds is associated with recombination of genetic factors located in the dissimilar parental chromosomes the proof can no longer be questioned. This last demonstration has been made in *Drosophila* and *Zea Mays* and will now be described.

(i) Females of *Drosophila* were taken having, in the first place, two *structural* differences between different parts of their X chromosomes (*viz.*, attachment and non-attachment of Y' (Fig. 14); fragmentation into two parts, one of them attached to the fourth chromosome and non-fragmentation; and, in the second place, two *gene* differences. They were crossed to males having a single normal (*i.e.*, non-fragmented and non-attached) X chromosome with the two corresponding genes recessive. The gene differences immediately adjoined the two structural differences, so that, in examination of the offspring, if crossing-over was seen to have taken place in an oöcyte by the character of the individual derived from it, new chromosome types having the two kinds of structure at each end of the X chromosome should be found cytologically in that individual,

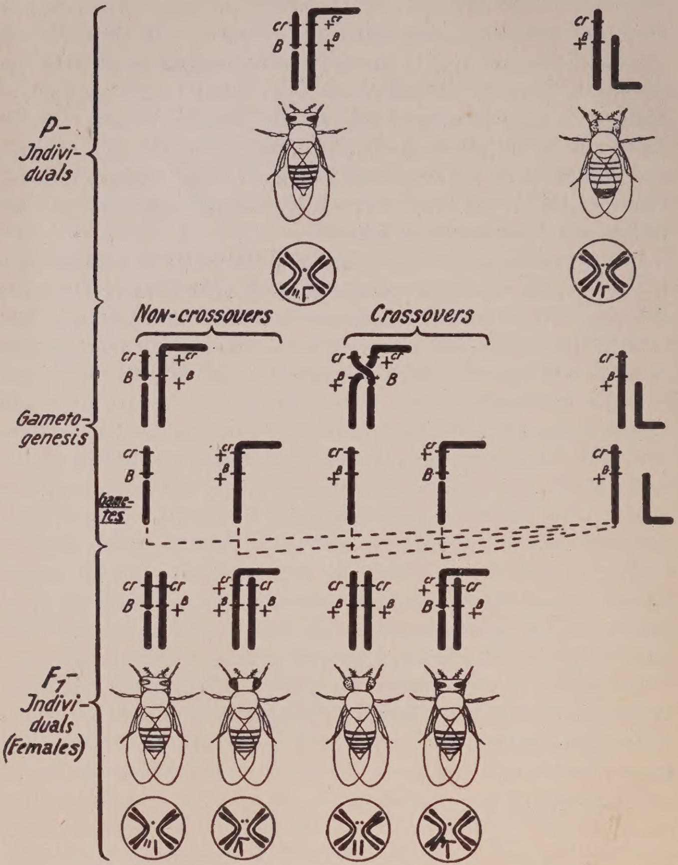

P-Individuals
Non-crossovers
Crossovers
Gametogenesis
Gametes
F1-Individuals (Females)
cr
B
+cr
+B

FIG. 70.—Diagram illustrating an experiment to show that exchange of segments is correlated with genetic crossing-over (for chromosome types, *cf*. Fig. 14). Top left: female with "bar" and "carnation" eyes. Top right: normal male (with Y'' chromosomes which can be neglected). Below: the chromosome complements and body characters of females produced with and without exchange of segments. (From Stern, 1931.)

and where no evidence of crossing-over was seen the maternal type should be found. This was tested in four experiments. Crossing-over with formation of new chromosome types was found in 156 flies ; no crossing-over was found with no new chromosome types in 203 flies ; two unexpected types were found and three contrary to expectation ; these are believed to be due to errors of genetical recording such as cannot be eliminated entirely (Stern, 1931). This is the most ambitious and successful attempt that has ever been made to correlate genetic and cytological observation.

(ii) An interchange and reduplication heterozygote in maize was recognised by its having a ring of four chromosomes, one of which had a small extra segment seen at prophase of meiosis. When this was crossed back to a form homozygous in respect of both the interchange and the reduplication the progeny could be classified cytologically according to the observed occurrence of crossing-over between the point of interchange and the point of reduplication. They could also be classified genetically according to the occurrence of crossing-over between factors known on previous evidence to occur in the segment between the interchange difference and the reduplication difference. The two classifications agree to the extent that would be predicted from the previously known linear order of the factors studied (Creighton and McClintock, 1931).

These experiments leave no doubt, in the first place, that exchange of segments occurs between dissimilar chromosomes in hybrids, and, in the second place, that it is associated with genetic crossing-over, as predicted on the assumption that the one determines the other. It is the minimum proof of the conditions of crossing-over and it is valid on the minimum assumptions.

The occurrence of all " secondary " structural changes (p. 243) in the chromosomes of hybrids is cytological evidence of crossing-over in so far as other causes of change can be eliminated.

The new chromosome types believed to result from pairing in the haploid (Ch. IX) fall in this category. The following special examples may be mentioned :

(iii) Half-mutants occur in the progeny of ring-forming *Œnothera* species. They have different pairing configurations from their parents as a result of segmental interchange (Ch. XIV).

Since this interchange occurs with definite frequency, to give 1 in 2,000 mutant offspring, and at a definite point, to give offspring of constant genetic and cytological properties, it has been argued that this is the result of crossing-over between relatively translocated segments in different chromosomes of the ring. Such crossing-over has since been shown cytologically in ring-forming *Œnothera* (*v. infra*).

(iv) Hybrids have been made between *Crepis* species having chromosomes of different shapes, and it would be expected that, crossing-over having taken place between them in the first generation, chromosomes of new shapes would appear in the second. Such new chromosomes have been found in the progenies of two triploid *Crepis* hybrids ; *C. capillaris* × *C. aspera* (Nawaschin, 1927) and *C. capillaris* × *C. tectorum*, *CCT* (Hollingshead, 1930 *b*). In the first, a chromosome of *capillaris*, in the second, one of *tectorum*, had lost a portion of one arm. In both it is to be supposed that the conditions of zygotene pairing in the triploid, where one thread at any point is unpaired, had rendered possible crossing-over between relatively translocated segments. Evidence that such crossing-over occurs in the triploid with segregation of cross-overs and non-cross-overs is found in the fact that the derived tetraploid (*cf.* Table 26) is a weak plant unlike any tetraploid produced by simple doubling.

(v) The attachment of the *X* and *Y'* chromosomes in *Drosophila* occurs always in the same way and, like the half-mutants, with a definite frequency, once in 1,500 to 2,000 times (Stern, 1929 *a*). Since the association occurs at a point where the two chromosomes are probably homologous, it is possible that it arises through crossing-over (*cf.* D., 1931 *a*, and Fig. 14).

(vi) Secondary structural changes have been observed in structural heterozygotes produced by X-raying in *Drosophila* (Muller, 1930 *a*). The progeny were deficient and redundant in small parts of chromosomes.

(ii) Proof of When and Where Crossing-over Occurs. The most direct proof is that resting merely on the axiom of permanence. A single interstitial chiasma between chromosomes both of whose corresponding ends are morphologically distinguishable proves crossing-over to have taken place between the four chromatids. Such direct evidence is provided by observation of pairing between dissimilar chromosomes in a *Festuca-Lolium* hybrid (Peto, 1932), but the chiasma is not directly demonstrable. The two following methods are analogous. They consist in showing that sister chromatids are united on both sides of a demonstrable chiasma and that therefore crossing-over has taken place at the chiasma.

(*a*) ON DEVELOPMENTAL ASSUMPTIONS. (i) *Localised Pairing in* Mecostethus (Janssens, 1924). The distal ends of the chromosomes do not pair; the proximal ends can be recognised constantly by the single polar granule on each. Since a chiasma is formed between the two the exchange of partner observed must follow crossing-over between two chromatids of the two chromosomes in the neighbourhood. McClung (1927 *b*) and Belar (1928 *b*) have doubted the developmental assumption that all four ends remain free throughout the prophase, but the assumption is plausible because it explains the localisation of chiasmata in this genus and in *Fritillaria*.

(ii) *Quadrivalent Pairing in* Hyacinthus (D., 1930 *b*). The chromosomes associate in pairs at pachytene in a tetraploid with exchanges of partner at random. These exchanges of partner are exchanges of whole chromosomes. When one chromosome forms a chiasma on either side of an exchange, *i.e.*, with two different chromosomes, it must consist of two sister chromatids. If therefore a chiasma arises between two chromosomes, one of which has a chiasma on either side with a third, then this chromosome consists of sister chromatids on both sides of its middle chiasma, and crossing-over must have occurred at that chiasma. Such configurations have been found not only in *Hyacinthus* but also in *Primula sinesis* (D., 1930 *a*), *Rosa* (Erlanson, 1931), *Campanula* (Gairdner, and D., 1931). Similar configurations were earlier observed in trivalents of triploid *Tulipa* (Belling, 1929; Newton and D., 1929), but could not be considered conclusive because there was a remote possibility that all three chromosomes in a triploid might conjugate successively (in time) at pachytene. This is inconceivable in a tetraploid, since the association of four is symmetrical and alternative attractions

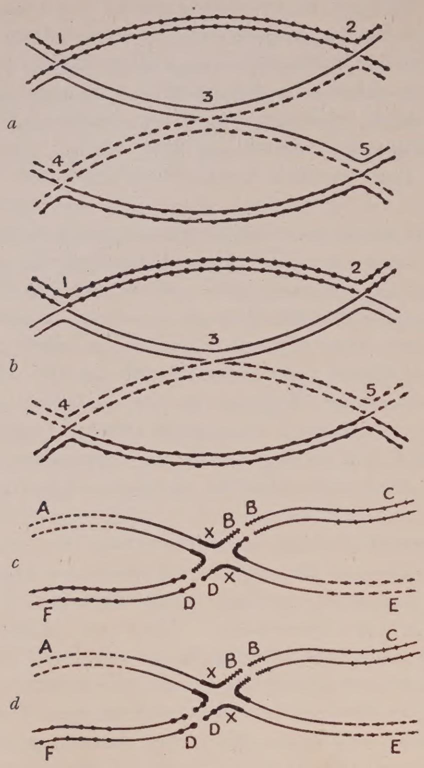


FIG. 71.—Diagram of chromatid structure of configurations showing a genetical interpretation on the classical assumption that no crossing-over has preceded chiasma-formation (*a* and *c*), and on the chiasma type assumption that chiasma-formation has been preceded and determined by crossing-over (*b* and *d*).

a and *b*, the quadrivalent configuration in *Hyacinthus*. *c* and *d*, the interstitial chiasma between homologous parts (*X*) intercalated in non-homologous chromosomes in *Œnothera* and *Pisum* (*cf.* Plate IV).

Note.—*a* is impossible because it demands the association of three chromosomes at pachytene; *c* is impossible because it demands association of non-homologous chromatids.

amongst chromosomes therefore equivalent (*cf.* also D. and Mather, 1932).

The assumption necessary for this proof's validity is that two chromatids at metaphase are derived from one chromosome at pachytene and that the chromosomes associate only in pairs at any one point at this stage.

(*b*) ON PHYSIOLOGICAL ASSUMPTIONS. (i) *The Figure-of-Eight.* Just as it is possible to infer crossing-over from the occurrence of a chiasma between two homologous segments intercalated in two chromosomes all four of whose ends are morphologically distinguishable, so it is possible to infer it where in these circumstances all four ends are physiologically distinguishable. The conditions have been found in interchange heterozygotes in *Œnothera* (D., 1931) and *Pisum* (E. R. Sansome, 1932) with rings of six and more chromosomes. (They might as well be found in homozygous forms with reduplicated segments, but that exceptional crossing-over is less likely in homozygotes.)

These forms are both strictly disomic so far as the chromosome ends are concerned, for they never associate otherwise than in pairs by single terminal chiasmata. Yet two chromosomes which are not associated terminally at either end are found associated by an interstitial chiasma ("*X*" in Fig. 71). Now the segments *B* and *B* are homologous since they are pairing, the segments *D* and *D* are also homologous. Therefore *B* and *D* are dissimilar. Therefore the two chromatids which are similar at *A* are dissimilar at the opposite end, and one of them must have crossed over.

Expressing this in a different way, we may say that since *B* and *D* are dissimilar the chiasma at *X* has arisen by the opening of reductional loops on both sides and not through the opening of an equational loop on one side and a reductional loop on the other (as on the classical theory). Therefore, crossing-over has occurred to determine the formation of the chiasma.

The figure-of-eight has also been observed in *Rosa blanda* (Erlanson, 1931) and *Datura stramonium* (Bergner and Blakeslee, 1932), probably with the same explanation, and the ring-of-four in *Trimerotropis citrina* constitutes a proof of crossing-over on similar assumptions (Fig. 72B, *v.* Ch. V).

(ii) *Interstitial Chiasmata in the Haploid.* Amongst the exceptional pairs formed in the haploid *Œnothera blandina,* Catcheside (1932) finds some with lateral chiasmata as in the unequal chromosome pairs of *Phrynotettix* (Fig. 75). Since the arm distal to the chiasma has nothing corresponding to it, it must be derived

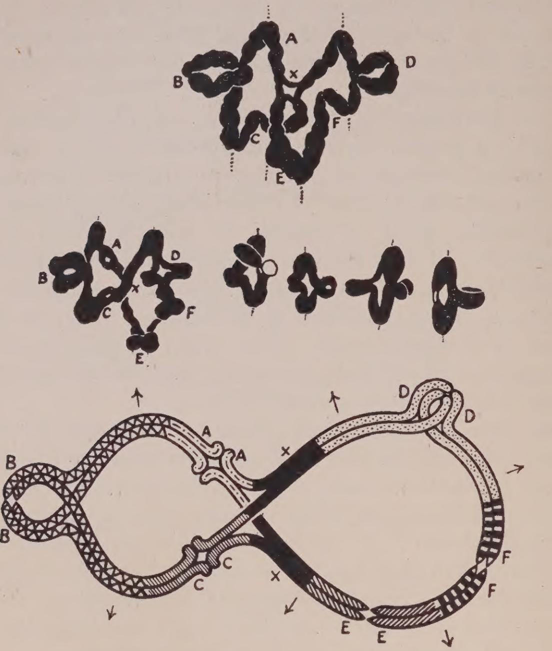


FIG. 72A.—The "figure-of-eight" in *Pisum* at first metaphase. Above, the configuration with its segments labelled. Below, a chromatid diagram of the same (*cf.* Plate IV). Between, the same type of configuration with the four simple pairs. The six chromosomes before crossing-over had the constitution: AB-BC-CXD-DF-FE-EXA. Crossing-over has given two new chromatids (or "daughter-chromosomes"): AXD and CXE (*cf.* Ch. XIV, from E. R. Sansome, 1932.)

Note.—The chiasma formed in the *X* segment is represented as having been arrested in terminalisation by the change of homology (*v.* p. 321).

from one parent chromosome. Since the proximal arms of the two chromosomes are derived from different members of the haploid complement each must consist of a pair of chromatids derived from the same parental chromosome. Therefore crossing-over must have occurred between a pair of chromatids from opposite chromosomes to permit of this chiasma being formed.

It may be objected to this proof (as well as to the preceding two) that the crossing-over might be due to a second chiasma being inevitably formed and immediately broken in the neighbourhood of the observed one. The observation of the critical configuration in two-thirds of the *Pisum* cells, however, makes this improbable assumption even more improbable, while the permanence of chiasmata as determining the association of chromosomes has been demonstrated in *Hyacinthus* (Ch. IV). And, finally, there are

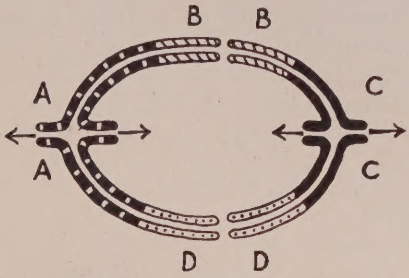


FIG. 72B.—Diagram showing the genetic relationship to be inferred in the chromatids of the ring of four found in *Trimerotropis citrina* by Carothers (1931). The arrows indicate the spindle attachments, which are terminal. The pairs in the homologous segments (A and A, C and C) being closest together are lying axially in the spindle. The fact that the B and D segments are lying equatorially proves that there is a chiasma in A and in C. Since B is not homologous with D nor C with A, these must have been crossing-over between the spindle attachments and the points of interchange, as shown in the diagram unless chromatids of opposite chromosomes are associated at the spindle attachment. This is associated with the formation of a chiasma in each case.

Note.—This ring, unlike the normal type, will have the second division reductional and the two chromosomes dividing at random will give 50 per cent. of non-disjunctional progeny.

special reasons given above for believing that chiasmata never break interstitially.

3. CYTOLOGICAL EVIDENCE OF CROSSING-OVER

(i) **From Anaphase Separation of Chromosomes.** Three characteristic anaphase observations are perhaps significant in relation to crossing-over. 1. Two of the four chromatids taking part in a chiasma and belonging to opposite chromosomes and opposite distal arms often show a constriction at anaphase at the position of the chiasma (Figs. 28 and 29). If the chromosome pellicle is weak at the point at which the break has occurred just before in crossing-over, this is precisely the result to be expected (Janssens, 1924; Belar, 1928 *b*, on living cells of *Stenobothrus*). 2. The arms separating distal to the chiasma often show a lightly staining connection in the neighbourhood of the chiasma, or the connection appears to oppose some resistance to separation (*Stenobothrus*, Janssens, 1924; *Hyacinthus*, D., 1929 *b*). This, occurring in organisms with little terminalisation movement, indicates the existence of a pellicle which surrounds sister chromatids and has to be broken in the separation at anaphase in such organisms where crossing-over has occurred. 3. Two kinds of separation of compensating chiasmata have been observed at anaphase (Fig. 29) in *Stenobothrus* (Janssens and Belar, *l.c.*), *Fritillaria Meleagris* (Newton and D., 1930) and *Pisum* (Pellew and E. R. Sansome, 1931). One kind separates with interlocking of chromatids, the other without interlocking. Since there are two genetic kinds of compensating chiasmata expected on the chiasmatype theory (*v.* Fig. 68) it is possible that these correspond to the two cytological types.

(ii) **From Prophase Interlocking of Chromosomes.** With few exceptions the chromosomes are fortuitously distributed in the nucleus before they pair at the prophase of meiosis, with regard to their homology. In the Diptera (*cf.* Metz and Nonidez, 1924) the homologous partners probably lie next to one another at the telophase of the preceding division owing to somatic pairing (*q.v.*) and persist in this relationship until zygotene. Apart from such exceptions it would therefore be expected that the chromosomes in pairing would often interlock, a strange chromosome passing through a loop between associations of the two homologues. Necessarily, this would only be detectable in favourable material. Interlocking has been seen taking place at zygotene in *Dendrocœulm* (Gelei, 1921) and *Viviparus* (Belar, 1928 *b*) and maintained at metaphase, in organisms with and without polarisation of the zygotene nucleus (*e.g.*, *Stenobothrus* and *Hyacinthus*), and in organisms with all degrees of terminalisation.

The detection and analysis of interlocking at metaphase is of importance, for the form it assumes will distinguish between various theories of chromatid relationship in organisms with and without terminalisation (Gairdner and D., 1931). On the hypothesis of chiasmatype crossing-over the chromatids derived from one parental chromosome fall apart together at diplotene so that an interlocked chromosome will lie between the separated chromosomes in the diplotene loops. On the classical theory the chromatids equally often separate equationally: in these cases an interlocked chromosome would be held between the paired *chromatids* of the other chromosome at diplotene. Such interlocking has never been observed.

Again, if chiasmata ever break in the course of terminalisation they would be expected to break where an interlocked chromosome passes through a loop which this movement is reducing. If, on the other hand, they never break, they should push the interlocked chromosome towards the ends and hold it if the ends are associated by a terminal chiasma. This seems to happen in *Œnothera* and *Campanula* and its observation supports the chiasmatype theory (D., 1931 *b*; Gairdner and D., 1931).

Interlocking should be classifiable on the chiasmatype hypothesis into three types at metaphase in an organism with terminalisation, according to whether the chiasmata formed by the interlocked chromosomes are moving away from the point of interlocking in both, one or neither of the pairs thus (Fig. 73) :—

(i) *Proximal Interlocking*. The chiasmata move away from the point of interlocking in both pairs of chromosomes, owing to its being near their attachment constrictions.

(ii) *Distal Interlocking*. The chiasmata on either side of the interlocking move in the same direction, *i.e.*, towards one end, in both of the interlocked pairs, owing to the interlocking being distal to the most proximal chiasma.

(iii) *Proximal-distal Interlocking*. The interlocking is proximal as to one pair and distal as to the other.

The distinction between this type and the second cannot be expected to be made in practice. Both will appear, in an organism with complete terminalisation, indistinguishable from a multiple chiasma except in the most favourable material. They may both therefore be described as distal.

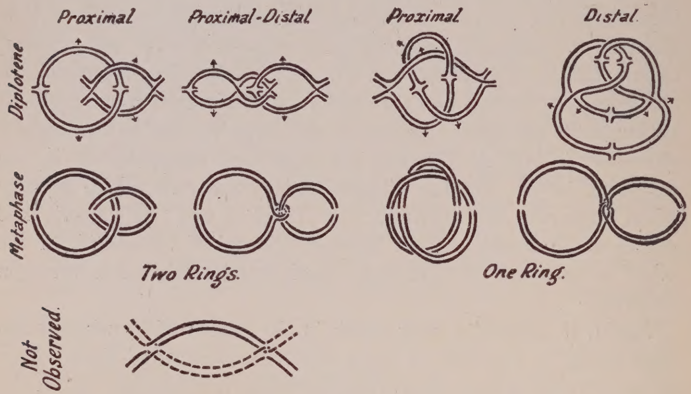


FIG. 73.—Chromatid diagram of diplotene and metaphase configurations showing interlocking of pairs of ring-bivalents (left) and within a ring-of-four (right) before and after terminalisation. The type not observed shows two types of association such as Janssens imagined might result from "total chiasmatypy" with crossing-over between both pairs of chromatids.

These kinds of interlocking should be found between separate pairs of chromosomes and between separate chromosomes of multiple rings, in interchange heterozygotes and polyploids.

A classification of the available observations based on these views shows that all the types that are expected on the chiasmatype hypothesis are found, and none that are not expected.

TABLE 44

Interlocking of Chromosomes at Meiosis

A. IN ORGANISMS WITHOUT COMPLETE TERMINALISATION (the distinction between proximal and distal being unimportant).	
(i) Between single pairs:	
Stenobothrus lineatus	Belar, 1928.
Hyacinthus orientalis	D., 1929 *b*.
Rosa blanda	Erlanson, 1931 *b*.
(ii) Within a multiple ring:	
Pisum sativum	Pellew and E. R. Sansome, 1931.
B. IN ORGANISMS WITH COMPLETE TERMINALISATION.	
(i) Between single pairs or multiple rings:	
(*a*) Proximal:	
Salamandra maculosa	Schreiner, 1906 *b*.
Œnothera spp.	Hoeppener and Renner, 1929. Håkansson, 1930, *a* and *b*. Catcheside, 1931 *b*.
Datura sp.	Blakeslee, 1929 (diagram).
Campanula persicifolia	Gairdner and D., 1931.
(*b*) Distal:	
Œnothera biennis	Cleland, 1923; D., 1931 *c*.
Campanula persicifolia	*l.c.*
(ii) Within a multiple ring (only in interchange heterozygotes).	
(*a*) Proximal:	
Œnothera biennis	D., 1931 *c*.
Campanula persicifolia	*l.c.*
(*b*) Distal:	
Pisum, Œnothera and Campanula.	

Note.—If the terminalisation of two compensating chiasmata were arrested by a change of homology (*v.* p. 321) an interlocking of chromatids within the bivalent should be produced in a proportion of cases, as it is produced in the separation of bivalents with such chiasmata at anaphase (*v. supra*). This result is possibly obtained in some of the figure-of-eight configurations in *Pisum* (E. R. Sansome, 1932).

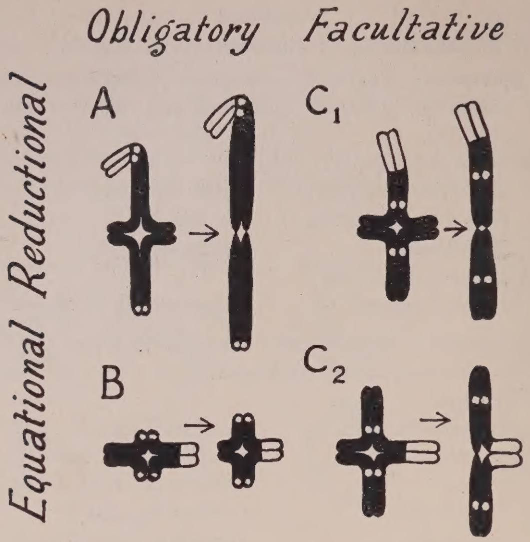


FIG. 74.—Diagram showing different types of division of unequal chromosomes owing, on the assumption of chiasmatypy, to the different relationships of the inequality, the spindle attachment and the chiasma, which may or may not be formed between them. (Where several chiasmata are formed the possibilities are more numerous.) The arrows represent the direction of the change undergone by the bivalent between diplotene and metaphase with terminalisation (incomplete in *B*). The inequalities and the points of spindle attachment are shown blank. *A*, first division regularly reductional owing to the attachment lying next to the inequality. *B*, first division regularly equational (second division reductional) owing to the attachment lying at the opposite end from inequality and one chiasma being formed between them. *C*, first division reductional or equational according to whether a chiasma is formed on one side of the attachment or the other. C_2 shows one of the two types of lateral chiasma (*cf*. Fig. 80). A, *Trimerotropis, Circotettix, Acridium Stenobothrus*, all sex chromosomes (and autosomes fused with sex chromosomes). B, *Phrynotettix*, chromosome " B "; C, *Phrynotettix*, chromosome " C "; *Mecostethus gracilis* and *Trimerotropis citrina* (Carothers, 1931).

(iii) **From the Segregation of Unequal Bivalents** (*v*. Table 21). Where chromosomes of different size or shape pair at meiosis, the dissimilar chromosomes might pass to the opposite pole at the first division (pre-reduction) or dissimilar pairs of chromatids might pass to each pole and separate at the second division (post-reduction), or either of these events might occur with the same bivalent in different cells. This expectation holds equally on either the classical or the chiasmatype hypothesis. But while the expectation cannot be more precisely defined in the case of the classical hypothesis it can be very precisely defined in the case of the chiasmatype hypothesis, for the two chromatids associated at the spindle attachment always pass to the same pole, and on this hypothesis the associated chromatids at diplotene are always those derived from the *same* parental chromosome, a rule which still applies to the spindle attachment at metaphase even with terminalisation. The division of unequal bivalents therefore provides a test of the chiasmatype hypothesis.

Its requirements with regard to the inequality are as follows :—

(i) Where no chiasma is formed in the segment between the spindle attachment and the inequality, the first division must be reductional.

(ii) Where one chiasma is formed between them, the first division must be equational.

(iii) Where more than one chiasma is formed between them, either result may obtain.

All unequal bivalents follow one of the first two types, or, where the position of the chiasma relative to the attachment and the inequality is variable, either of them. Sex chromosomes fall exclusively into the first class, probably for the reason that the inequality includes the spindle attachment, and there can therefore be no chiasma between them. Thus there are, in accordance with the chiasmatype hypothesis, three types of unequal bivalents in regard to their mode of separation at the first division (*v*. Fig. 74) : A. Those in which the spindle attachment is next to the inequality ; they always divide reductionally. B. Those in which the attachment is at the opposite end to the inequality ; they always divide equationally where one chiasma is formed ("B" and "C_3" in *Phrynotettix*). C. Those in which the attachment is part way towards the end from the inequality ; they reduce either at the first or at the second division according to the position of the chiasma (C_1 in *Phrynotettix*).

It must be assumed that Wenrich's unequal chromosome pair "C_1" has a median spindle attachment. Wenrich's assumption that it is terminal and sometimes at one end, sometimes at the other, is unparalleled and is not required by *either* hypothesis. The occurrence of a chromosome with a submedian spindle attachment and forming one chiasma sometimes in one limb and sometimes in the other is, on the other hand, justified by analogy with chromosome 7 in the related *Circotettix* (*cf.* Table 50 and Fig. 82).

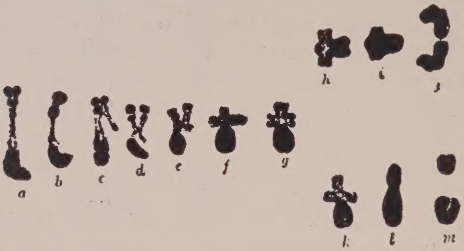


FIG. 75.—The development from pachytene to anaphase of the unequal bivalent "C_1" in *Phrynotettix*. (From Wenrich, 1916.) Wenrich supposed that the figures *h*, *i*. *j* and *k*, *l*, *m* were alternative derivatives of *g*. The present theory is that *d*, *e* and *f* would give *h*, while *c* and *g* would give *l* owing to the different position of the chiasma.

Unequal bivalents with chiasmata between the spindle attachment and the inequality should, on the classical hypothesis, give lateral chiasmata of the type shown in Fig. 79 in a proportion of nuclei; but they never do. Small fragments, on the other hand, pairing with major chromosomes always give this type of lateral chiasma (Ch. V). This would result, on the chiasmatype hypothesis, from the third type of chiasma relationship if the two chiasmata were regularly compensating (*i.e.*, from double crossing-over in two chromatids or from single crossing-over in all four). Special conditions determining such crossing-over in these cases, where the spindle attachments of the pairing chromosomes do not correspond, would account for the difference on the chiasmatype hypothesis, while on the classical hypothesis, like all other special chiasma relationships, it necessarily remains unaccountable.

4. EVIDENCE BY PARALLEL INFERENCE FROM CHIASMATA AND CROSSING-OVER

Evidence showing a parallelism between frequencies and distributions of chiasmata and variations in these, on the one hand, and similar properties of occurrences of crossing-over on the other, supports a hypothesis relating chiasmata to crossing-over. Such "general evidence" can now be considered.

(i) **In Diploids (General).** In organisms with chromosomes of uniform size the average frequency of chiasmata in each diplotene bivalent is, so far as we know, usually between one and three. In *Primula sinensis* it must be greater than two, and is probably less than three. Where large size-variations occur the larger chromosomes have a higher average frequency or it ceases to be proportional to the length. In certain Liliaceæ and Leguminosæ the chiasma frequency is greater than 3; in the Tettigidæ it seems to be usually less than two. Further, where pairing is by chiasmata a single chiasma must always be formed to secure regular pairing.

These observations show definitely the amount of crossing-over to be expected in chromosomes in general and in particular instances, on the chiasmatype hypothesis. The average occurrence of one chiasma must correspond to 50 per cent. of cross-overs in the length of chromosome in which it occurs, *i.e.*, to 50 corrected units of crossing-over distance. Therefore the lengths of chromosomes completely measured in cross-over units should be greater than 50, and it should frequently be over 100.

The following table shows the measurement of those chromosomes of organisms whose mapping in units of crossing-over may be taken to be fairly complete :—

Drosophila melanogaster (three of the four groups).	70 (*X*), 102 (*III*), 107 (*II*) (*cf.* Morgan, 1925).
Zea Mays (eight of the ten groups).	70, 90, 95, 100, 110, 120, 120, 160 (*cf.* Brink and Cooper, 1931).

No chromosome has been definitely measured and found to have a length of less than 50 units. If the pairing of the small fourth chromosome in *Drosophila melanogaster* is due to chiasma formation the chiasmata would need to be strictly localised and map distances would not have the same relation to length as in the other chromosomes. Two factors close together in this chromosome would give 50 per cent. crossing-over. The small cross-over values obtained in the fourth chromosome are apparently explicable as the result of non-disjunction. Its genetical map is therefore still in doubt, and the possibility that it is really 50 units long cannot be dismissed. The frequencies of crossing-over observed therefore agree with expectation on the chiasmatype hypothesis so far as the limited comparative data go (*cf.* Sect. (v) and Fig. 78).

(ii) **In Polyploids.** *Distribution among the Chromosomes.* In non-hybrid triploids and tetraploids the chromosomes pair at random and form chiasmata at random, *i.e.*, any one chromosome may pair at different points with any of the other chromosomes with which it is homologous and form chiasmata with them (Newton and D., 1927). Similarly, crossing-over is at random amongst corresponding chromosomes in triploid *Drosophila* (Bridges and Anderson, 1925), and tetraploid *Primula sinensis* (De Winton and Haldane, 1931).

Structural Units. Gametes produced by triploid *Drosophila* with three homologous chromosomes have one or two of these; and when they have two they are sometimes identical in one part, although the three homologues all differed in this part; they are therefore derived from the chromatids of one chromosome. But the chromosomes are sometimes dissimilar in other parts; they must then be the result of crossing-over between chromatids, not between chromosomes. In genetical language, these "equational exceptions" are said to prove crossing-over in the "four-strand stage," *i.e.*, after division of the chromosomes into chromatids, and never between all four strands at the same point (Bridges and Anderson, 1925; Redfield, 1930; *cf.* Bridges, 1916). Such is the method of crossing-over demanded by the chiasmatype interpretation of the available cytological evidence.

A structurally abnormal type of *Drosophila* yields similar evidence.

Drosophila females with two *X* chromosomes "attached" at the spindle attachment end (*v.* Fig. 14) and differing in several factors have female progeny with both their *X*'s derived from the same egg-cell of the mother, and these show crossing-over. It is therefore possible to see the constitution of two of the four *X* chromosomes derived from the four chromatids of one maternal cell and know whether the crossing-over took place before the division into four or after, and whether there is a rule as to the assortment of the four chromatids. Thus, if the two chromatids had factors *ABCDE* and *abcde*, attached at *Aa*, it was found that flies appeared homozygous for recessive factors. Therefore, again, crossing-over must have taken place after division into chromatids, and between only two of the four, for otherwise crossing-over, being between whole chromosomes, would only yield complementary types, such as *ABCde* and *abcDE*.

Segregation. In the attached-*X* experiment, it was further found that the proportion of recessives was lower the nearer the factor considered was to the spindle attachment. The segregation of the chromatids is therefore determined at the spindle attachment (Anderson, 1925; *cf.* Bridges and Anderson, 1925). On this system of crossing-over and segregation, factors situated more than 50 units away from the spindle attachment should be freely assorted as between chromatids.

Rhoades (1931), however, found that the segregation was not entirely at random at the distal end of the *X*-chromosome (70 units away) as it should be. More than one-sixth of homozygotes appear. This means most probably that a disproportionately high amount of crossing-over occurs between chromatids continuing one another, and therefore passing to the same pole—for we are dealing here with crossing-over between two chromosomes which have become two segments of one chromosome.

This random segregation of chromatids where two chromosomes that have undergone crossing-over pass to the same pole at the first division means that the proportions of segregation expected in tetraploids will not always be in the simple proportions given by Muller for the assortment of chromosomes but will show a higher proportion of recessives. It will be possible for both divisions to be reductional in regard to a given part of a chromosome represented four times (Haldane, 1931 *a*; and *cf.* Fig. 84, factors *PPPp*). This random chromatid segregation will only be expected on the chiasmatype theory when factors are at the maximum crossing-over distance of 50 units from the spindle attachment. It is therefore strictly in accordance with this theory that the chromatid type of segregation has only been found in a small proportion of the cases investigated (Crane and D, 1932).

Frequency. The total frequency of crossing-over per chromosome in the triploid is the same as in the diploid, although the distribution is different (Redfield, 1930). This should mean that the total number of chiasmata per configuration is increased by half in the triploid. Exactly the same increase is found in triploid plants that have been compared with related diploids (*Tulipa*, D. and Mather, 1932; *Hyacinthus*, Stone and Mather, 1932, *v.* Sect. 5).

(iii) In Structural Hybrids. Observations of crossing-over in structural hybrids agree with expectations based on cytological observation if crossing-over is supposed to be conditioned by pairing of identical segments of chromosome at pachytene, as are chiasmata.

(*a*) *Translocation.* On this assumption, Dobzhansky's results (1931) show that the amount of pairing is reduced in the neighbourhood of a break in *Drosophila* heterozygous for a translocation. Where the break has occurred at a median attachment constriction of a chromosome it usually leads to a reduction of crossing-over in both arms. Where it occurs in one arm the reduction is stronger in the affected arm, while in the unaffected arm it is normal. Further, Dobzhansky has shown that this reduction is due to the interference of the newly associated segments with one another in pairing, for when a long segment of an autosome is translocated to the *Y* chromosome (which has no partner, at least for the greater proportion of its length), its crossing-over is not sensibly reduced. There is no interference. The conclusion that a change of linear homology hinders pairing is in accordance with cytological expectation, which demands a limited number of "pairing blocks," *i.e.*, a limited capacity for changing partner. When the translocated segment is short, its crossing-over is reduced. Evidently, therefore, the chance of two homologous segments pairing is decreased when the segment is less than a certain length. Since the fourth chromosome is shorter than any segment concerned, and yet pairs regularly, this decrease is clearly due to the change of association. This again is cytologically intelligible, for, with a limited number of pairing blocks, short segments cannot be expected to have an equal chance of securing a partner with long segments.

There is a reduction of crossing-over equally on both sides of the break, which indicates that pairing of the chromosomes may begin either distally or proximally to the break. This rule would therefore probably not apply to organisms with polarised chromosomes at the zygotene stage.

(*b*) *Inversion.* Similarly Sturtevant (1926 *b*) found that crossing-over was suppressed in inversion-heterozygotes between the normal and inverted sections of the chromosome, apart from the occasional occurrence of double crossing-over. Crossing-over takes place between the relatively inverted sections when they meet the opposite way round to the rest of the chromosome. Single cross-overs then give reduplication of the non-inverted sections, with non-viability. This observation therefore shows that pairing takes place only between homologous particles, a conclusion in agreement with cytological observation as well as with genetic theory.

(*c*) *Lateral Translocation.* Bridges (1917) showed that a fragment of the second chromosome about 8 units long had become attached to the third chromosome. Hamlett (1926) found that crossing-over in the affected region of the third chromosome was reduced in heterozygotes ; 20 units in the third chromosome were reduced to about 6, and a further 10 units to 3, while more remote regions were only slightly affected. This reduction resembled that in other translocations, but it was found equally in homozygotes. The only conclusion seemed to be that the translocated segment was attached laterally and the chromosome was branched (*cf.* Ch. III, 3 (iii)).

Inter-race hybrids in *Drosophila obscura* show a reduction of crossing-over as compared with the parents, which suggests a reduction in the length of chromosome paired as a result of structural hybridity, although the detailed character of the structural differences cannot yet be defined (Koller, 1932).

(*d*) *Interchange*. In plants having more than two chromosomes associated in a ring, chiasmata are formed in such a way as can only be derived from a radial pachytene association instead of the straight line type of association found in ordinary pairing both in diploids and polyploids (Fig. 40). The crossing-over map should therefore be radial or star-shaped (D., 1931 *c*). This prediction has been made independently and verified by observations on crossing-over between three factors in ring-chromosomes of *Œnothera* (Emerson, 1931; *cf.* Brink and Cooper, 1931).

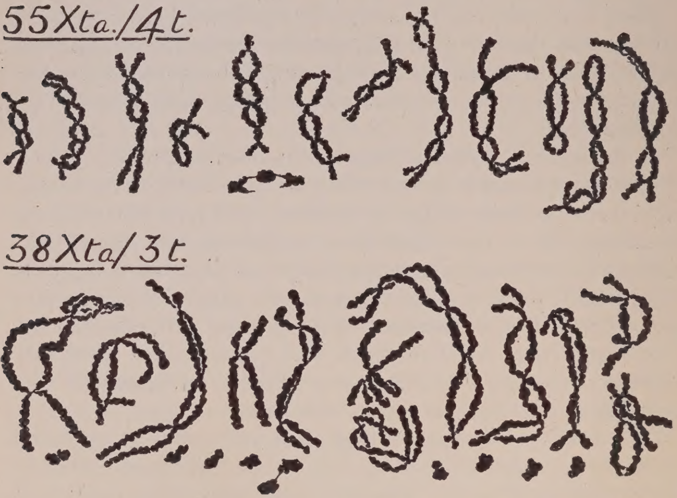


FIG. 76.—The twelve diplotene bivalents in two clones of *Fritillaria imperialis*, giving the total number of chiasmata and the number terminal in each. The upper one has three fragments united by a triple chiasma; the lower one has ten fragments, two of which are paired. *Cf*. Table 18 (from D., 1930 *c*).

In the progeny of interchange heterozygotes in *Drosophila*, Muller (1930 *b*) found that the interchanged segments had usually passed to opposite germ-cells at reduction as in a ring in *Œnothera*.

The reduction of crossing-over in structural hybrids is paralleled by the reduction in the number of chiasmata formed and in the amount of metaphase pairing in structural hybrids both defined and undefined (Chs. V and VI).

(iv) **Conditions of Variation.** The frequency and distribution of chiasmata and of crossing-over are liable to variation subject to environmental, genetic and developmental conditions.

(*a*) OBSERVATIONS OF CHIASMATA. The chiasmata in the *m* chromosomes of *Vicia Faba* (Maeda, 1930 *b*) show a different frequency variation at metaphase in different preparations. This is to be ascribed to an environmental or developmental difference (Fig. 77). The same conclusion can be derived on the chiasma theory of pairing from the variations of pairing in *Triticum* hybrids (Kihara, 1929 *c*), and the parallelism supports this theory.

The chiasma frequency differs in different clones of *Fritillaria imperialis* (Fig. 76 and Plate VI). The highest mean frequency at diplotene is 5·2, the lowest 3·0. This is a regular property of each clone, irrespective of the time of preparation, and is therefore assumed to be genetically determined. Different forms of *Tulipa australis* show a different degree of concentration in chiasma frequency, *i.e.*, different interference (*v. infra*). This modification of chiasma distribution is probably genetically determined (D. and Janaki-Ammal, 1932). Chiasma formation may also be genetically suppressed (Ch. XIII).

(*b*) OBSERVATIONS OF CROSSING-OVER. The frequency of crossing-over is modified by changes : (*a*) in external conditions, *e.g.*, temperature (Plough, 1917 ; Kirsanow, 1931, on *Drosophila* ; *cf.* Stern, 1928) and irradiation (Muller, 1925) ; (*b*) in development, *e.g.*, crossing-over varies with the age of the female in *Drosophila* (Bridges, 1929) ; (*c*) in genotype, *e.g.*, factors occur reducing crossing-over and modifying its distribution (Detlefsen and Clemente, 1923 ; Bridges, 1929), or altogether suppressing it (M. S. and J. W. Gowen, 1922, 1928 ; Anderson, 1929).

Most changes in crossing-over frequency are differential with regard to different parts of the chromosome, or, we may say, change in frequency is correlated with change in distribution. Thus reduction in crossing-over frequency is attended by an increase in the neighbourhood of the spindle attachment.

The genetic suppression of crossing-over is probably of two kinds :—

Gowen (1928 *et alibi*) and Bridges (1929) found that with suppression and reduction of crossing-over by autosomal factors in the female the fertility of the female was reduced, and that this was associated with irregularities in the pairing of the chromosomes. The factor had no effect on the male. This means that the male character of localisation of chiasmata (if such it be) inhibited the effect of the factor for crossing-over suppression.

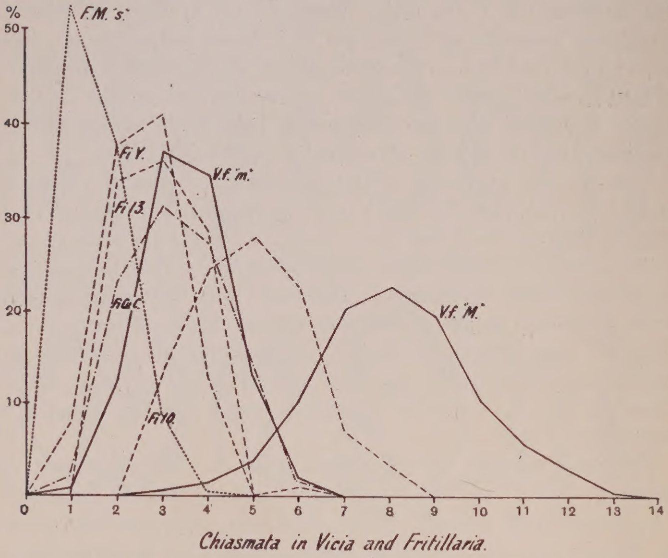


FIG. 77.—Chiasma frequencies in the bivalents of *Fritillaria Meleagris*, *F. imperialis* (various clones), and *Vicia Faba* (" m " and " M " types of chromosome), showing decreasing interference values with the higher mean values. (From D., 1931 *c*.)

Anderson (1929) also found that reduction of crossing-over by an *X*-chromosome factor in the female was associated with irregularity in the pairing of the chromosomes. But this factor rendered the male sterile as well. Evidently the male character did not inhibit the crossing-over reduction. As will be seen later, it is most important to find that this can occur, because it indicates that the processes determining pairing are analogous in the male and the female.

This difference in genetic relationship with the male character may indicate a difference in the *modus operandi* of crossing-over suppression, the first factor working to reduce the length of chromosome paired, the second, to reduce chiasma frequency, for the one is found to increase crossing-over in the attachment constriction end, the other to reduce it. It will be seen later that it is possible to identify these two separate causes of failure of pairing (Ch. XIII).

(v) Linear Distribution. (*a*) IN RELATION TO ONE ANOTHER (INTERFERENCE). A statistical examination of chiasma frequencies in bivalent chromosomes of *Vicia, Fritillaria, Rosa* and *Tulipa* shows that their distribution is too great near the mode and too little near the extremes on an expectation of randomness (Haldane, 1931 *b*).

This means that the occurrence of one chiasma reduces the chance of occurrence of another in its neighbourhood. Chiasmata show " interference " like that shown by cross-overs. It should be noted that the distribution in position in the chromosome of chiasmata may be random (and apparently is in many organisms), although their distribution in frequency and in relation to one another is not so.

On the classical theory that chiasmata arise through the meeting of equational and reductional loops this rule is inexplicable. On the chiasmatype theory (crossing-over being the cause of chiasmata), it may be regarded as due to crossing-over locally reducing the condition of stress (such as torsion among the paired threads) which has actually promoted it (*v. infra*).

A second method of observing interference has been attempted by Belling in observing internode lengths. These distances, however, are likely to be determined more by the conditions of equilibrium in chiasma movement than by the original interference, for it is probable that movement occurs as soon as chiasmata are formed, in all organisms (Ch. XII). The frequency method is therefore the only one available for showing interference.

On any theory of crossing-over assuming a relationship with chiasma formation (whether as its cause or as its effect) this rule is related to the existence of interference of crossing-over between two chromatids with *either* crossing-over between the same two *or* crossing-over between any two. (The consequences of these assumptions have not yet been compared with genetic evidence.)

Little is yet known of the relative frequency of compensating and non-compensating chiasmata, but it is worth noting that genetic interference might have expressed itself merely in crossing-over being only between different chromatids at successive chiasmata, in which case non-compensating and reciprocal compensating chiasmata would not occur. The fact that such chiasmata do occur, and that interference is determinable from the frequencies of chiasmata, agree in showing that interference is a phenomenon affecting chiasmata as individual occurrences and not chromatids as individual structures.

(*b*) IN RELATION TO POSITION ("MAP-DISTANCE"). In some organisms the number of chiasmata formed in a bivalent is a direct function of the length of the chromosomes paired. This is so in *Vicia Faba* (*v.* Fig. 77), where the *M* chromosome with a mean chiasma frequency of 8·1 is a little more than twice as long as the *m* chromosomes with a frequency of 3·0. It is equally so in *Hyacinthus* (*v.* Ch. IV) and in *Fritillaria imperialis* (*v.* Ch. V), where the frequency of pairing of fragments is predictable on this assumption. The same generalisation can be applied to some organisms with localised chiasmata, *e.g.*, *Mecostethus* and *Fritillaria Meleagris*, on the ground that only the region near the spindle attachment is paired and can form chiasmata ; and this region is of the same length in all chromosomes irrespective of their total length. But in others this is not the case. In *Stenobothrus parallelus* (D. and Dark, 1932) with distributed chiasmata, the longer chromosomes with median spindle attachments are more than five times the length of the shortest, yet their chiasma frequency is only about three times as great. The same is true of *Hyacinthus amethystinus* (D., unpublished), *Syrbula acuticornis* (Robertson, 1916), and *Yucca flaccida* (O'Mara, 1931). In none of these three cases is there evidence of localisation. It would appear, therefore,

PLATE VI

FIGS. 1–3.—Meiosis in the oöcytes of the earthworm *Allolobophora*. (From Foot and Strobell, 1905, smears slightly pressed before fixation.)

Fig. 1. Diakinesis. Fig. 2. Early metaphase. Fig. 3. Full metaphase. Note terminal and interstitial chiasmata.

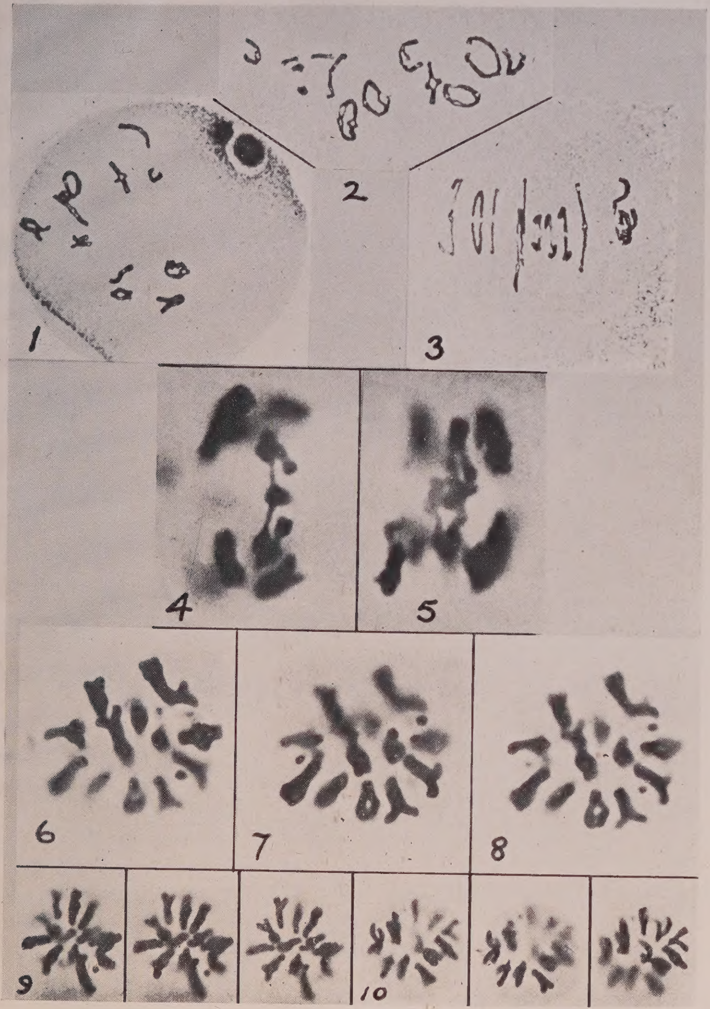
FIGS. 4 AND 5.—Anaphase of the first division in *Kniphofia* × 2000. (From Moffett, 1932 *a*.)

Fig. 4. Separation of bivalent with single interstitial chiasma. Fig. 5. Separation of bivalent with two compensating chiasmata leading to interlocking.

FIGS. 6–10.—First metaphase in *Fritillaria*, to show different distributions and frequencies of chiasmata (*cf*. D., 1930 *c*).

Figs. 6–8. *F. imperialis* "Yellow," 12 unpaired fragments. Fig. 9. *F. imperialis* "Crown upon Crown," more numerous chiasmata, 6 fragments. Fig. 10. *F. Meleagris*, few and localised chiasmata.

PLATE VI


1
2
3
4
5
6
7
8
9
10

[*To face p. 286.*

that here chiasma frequency is no longer a direct function of length, and that this and localisation were genetical adaptations necessary to the regular pairing of the short chromosomes alternative to a general increase in chiasma frequency, and to be expected wherever the chiasma frequency is low and considerable differences occur in length (Fig. 78).

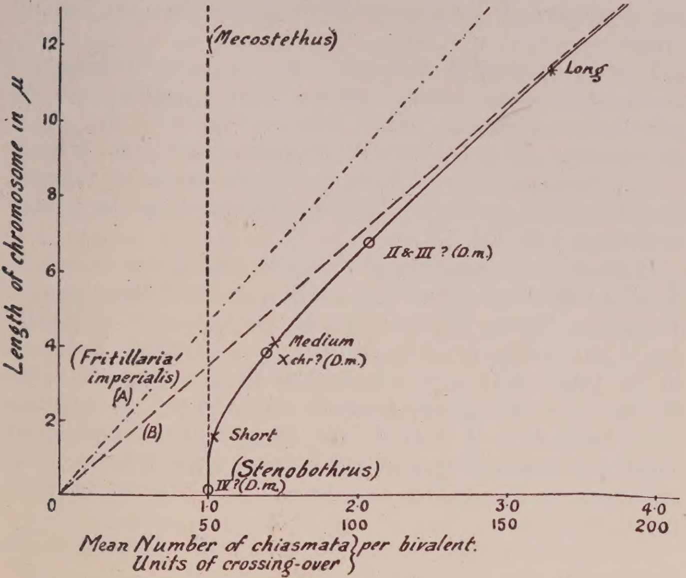


FIG. 78.—Graph showing three types of relationship possible between chiasmata or crossing-over and the length of the chromosomes: direct proportion in *Fritillaria imperialis* (two clones); fixed value with localisation in *Mecostethus* and perhaps in some *Tettigidæ*; the compromise in *Stenobothrus* and perhaps in *Drosophila melanogaster* "*D.m.*" (From D. and Dark, 1932.)

The possibility of testing an analogy to these observations in crossing-over frequencies is not yet available, but there are a few indications that similar departures from simple expectation occur. The *X* chromosome of *Drosophila melanogaster* is less than two-thirds the length of the longest chromosome, yet it has two-thirds of the map-distance length measured in crossing-over units. This is a departure in proportion in the direction expected from the analogy with *Stenobothrus*. A second indication is inconclusive; the *X* chromosome in *Drosophila Willistoni* (Metz, 1923) is twice the length of that in *D. melanogaster*, but its map length is only one-fifth greater.

Finally, the group of observations already referred to show that wherever there are special conditions affecting crossing-over, the distribution of crossing-over is affected relative to the spindle attachment. All such conditions must affect the relation of length to map-distance. There is therefore no special reason for expecting that under any particular conditions the one should be a direct function of the other.

If the chiasma frequency in *Drosophila melanogaster* is such an indirect function of chromosome length as in *Stenobothrus*, then the fourth chromosome, although extremely short, should be of 50 units' length, a condition which would not be easy to verify. But if one of the fourth chromosomes were attached to a fragment of the *X* chromosome the chiasma frequency should be reduced in the new triple body, $IV + X + IV.X$, and the small unattached fourth should frequently fail to pair, and therefore sometimes pass to the same pole as its attached homologue. This is found by Stern (1931).

Further observations on distribution will be considered in the next section.

5. EVIDENCE OF HOW CROSSING-OVER OCCURS

The question of the conditions determining crossing-over—the question of how it comes to take place—is necessarily much more speculative than the question of when and where it takes place, with regard to which proof has been given in special cases. As Janssens has remarked (1924, translation): "We know too little of the physico-chemical properties of the chromosomes at various stages of their development to dare to put forward here an opinion in so delicate a question." Considerations as to how crossing-over may conceivably take place have been offered by Belling (1928 *c*, 1931 *a*) and Sax (1930, 1931). These support the theory of crossing-over they agree with if that theory rests (as Belling's does) on any discriminating cytological evidence. But to use such considerations as evidence themselves of a theory of crossing-over otherwise unproved is putting the cart before the horse (*cf.* p. 343).

If crossing-over precedes and determines the formation of chiasmata, two kinds of evidence throw light on its origin. First, it must be supposed to occur at pachytene, and it is during this stage almost certainly that the final splitting of the chromosomes takes place (*cf.* Ch. X). It is possible therefore that it is the act of division of the two chromosomes at the time they are paired side by side that conditions the crossing-over between them.

Secondly, as Belling (1931 *a*) suggests, twisting of the threads at pachytene may promote crossing-over. Definite evidence in favour of this view now seems to be forthcoming in the cytological observations of interference referred to earlier. If breakage amongst the four threads associated at the end of pachytene is caused by torsion, reunion amongst the broken ends is most likely to occur in such a way as to relieve the strain. The occurrence of one break will therefore reduce the chance of another break in the neighbourhood. The interference observed is therefore expected on the theory of torsion. It should be noted that the torsion here suggested is not lengthwise like that imagined in the earlier expositions of crossing-over by Morgan and his collaborators, but crosswise, *i.e.*, not bending, but twisting.

The torsion hypothesis is supported by several theoretical considerations. In the first place, according to the precocity theory, diplotene looping is directly determined by the completion of the division of the two chromosomes into four chromatids. But crossing-over cannot occur before this division is complete. Nor can it occur after, on the chiasmatype theory, for it determines the formation of chiasmata. These hypotheses therefore require that crossing-over occurs *at the moment* of effective division. Now at this moment four thin strands replace two thicker ones. If, therefore, torsion determines crossing-over by breakage and reunion it is precisely at this moment that it should occur. It therefore seems unnecessary to assume, as Belling has done, that breakage at late pachytene is rendered especially easy by the successive elements or genes not being so effectively united as at a later stage.

In the second place the occurrence of crossing-over at the end of pachytene coincides with the beginning of the assumption of a spiral by the chromosomes. The condition of being paired appears to offer some resistance to the condensation in a spiral, for the unpaired parts of unequal bivalents (*e.g.*, in *Phrynotettix*, Wenrich, 1916; *Trimerotropis*, Carothers, 1931) condense in advance of the paired parts. The spiral can only be produced by such a condition of torsion as we are imagining. If then pairing resists the torsion while crossing-over relieves it and is facilitated by the chromosomes splitting, all the conditions will favour the occurrence of crossing-over. The question therefore arises: Can the same conditions be shown to influence the assumption of a spiral on the one hand and crossing-over and chiasma formation on the other?

Let us first examine the conditions of contraction in a spiral. The chromosome spiral seems to be a regular one. Were it to change direction in the middle of a chromosome arm an otherwise unaccountable irregularity would be expected in the outline of the chromosome such as is never observed at mitosis or meiosis. A regular spiral implies that its development is directed or controlled from one point. This is presumably the spindle attachment, especially since differential precocity within the chromosomes is related to the spindle attachment in *Mecostethus* and the absence of a spindle attachment in new fragments in *Tradescantia* (D., 1929 *c*) seems to hinder their contraction. The simplest way in which this control could be exerted would be by a rotation or twisting of the thread, which would automatically induce a spiral form if the thread were enclosed in a pellicle offering some resistance to its rotation and free from the source of rotation. If the spiral arises in this way it should turn in the opposite direction on the two sides of the spindle attachment. This possibility has been tested in a remarkable way. The linear contraction is irregular in Navashin's ring chromosome (Ch. III), a result that might well follow the two contrary spirals meeting on the opposite side of the ring and counteracting one another.

Various kinds of evidence may be taken to point to the existence of a pellicle. A morphological distinction is often made between "chromatic" and "achromatic" parts of the chromosome. A genetical distinction may also be made between the genes and accessory materials or conditions in the chromosome (D., 1932). The artefacts on which the first distinction rests are sometimes not characteristic, but the following evidence seems to be valid:

(i) The chromosomes are discontinuously constructed, as seen both at prophase in the separation of chromomeres and at metaphase in the constrictions (Chs. II and IV). This structure is difficult to understand in terms of the properties of the genes themselves and suggest that the chromatid is held in a pellicle.

(ii) Two of the four chromatids of the anaphase bivalent sometimes show constrictions at the positions where crossing-over is assumed to occur (Ch. IV and p. 270), as though a pellicle were injured by the change.

(iii) The chromatids in separating at anaphase distal to a chiasma are held together at a point next to the chiasma, although their ends are often free, again as though they were held together by a pellicle.

(iv) The elimination of chromatin at the anaphase of the first division in oögenesis in some Lepidoptera (Seiler, 1923) cannot be supposed to be an elimination of permanent material, since it does not change the structure or number of the chromosomes in the derived nuclei.

(v) The property of differential precocity of certain chromosomes can scarcely be developed by a consistent change throughout the permanent materials (Ch. XIII).

(vi) The permanence of size differences in chromosomes that cannot be attributed to gene change must be regarded as genetic evidence of accessory materials in the chromosomes (Ch. III), though their relationship with the physically inferred materials must remain in doubt.

The circumstances controlling the origin and properties of accessory materials in the chromosome have so far escaped analysis. It has proved difficult to test them either by natural comparison or experiment. But it is not possible to deny that the chromosomes contain other materials than the genes. Some of the evidence points to the existence of accessory materials such as a pellicle with an organic continuity of its own. Other evidence points to the existence of material which is subordinate in its reproduction to that of the genes. And other evidence again, particularly that of differential condensation, may be equally interpreted as pointing to variation in the properties of the spindle attachment in its controlling functions.

" Spiralisation," as we may call it, may therefore be controlled by a reaction of the spindle attachment and a surrounding pellicle. The relationship of the spindle attachment to chiasmata and crossing-over has already been shown in various ways, but certain special evidence is worth recalling. (i) Crossing-over and chiasma formation is as high in the individual chromosomes of triploids as of diploids (*v. supra*) although the length of chromosome paired is reduced. They may therefore be said to be proportional to the number of chromosomes as units, when these vary, and not to the lengths paired. This unitary action again suggests unitary control of the spindle attachment. (ii) In *Drosophila* crossing-over seems to be concentrated in the middle of each arm of the second and third chromosomes, and in the middle of the *X* chromosome (Dobzhansky, 1929, 1930 ; *cf.* Sansome and Philp, 1932). Its concentration therefore has the same relation to the spindle attachment in all the chromosomes. Moreover, it is this relation which is affected, as we have seen, when crossing-over is genetically reduced. (iii) The smallest chromosomes in *Stenobothrus parallelus* condense more rapidly than the larger ones. They also have a proportionately higher chiasma frequency. If the spindle attachment controls both, these results are to be expected, since its effects must be relatively concentrated in the absence of some special compensating effect.

These observations indicate a common control of chromosome contraction, of crossing-over, and of chiasma formation, in the spindle attachment which may be supposed to institute the torsion that determines them all. The problem of the causation of crossing-over is therefore one which it is becoming possible to approach from a less speculative point of view, using cytological evidence, and on the hypothesis that chiasmata are determined by crossing-over the variations in the frequencies and distributions of both are intelligible, as they cannot be on any other hypothesis.

Conclusion. The specific and general evidence outlined above is sufficient to justify us in taking the chiasmatype hypothesis, newly defined above, as a working hypothesis to relate genetical and cytological observations universally. It will therefore be assumed that wherever chiasmata are formed they result from crossing-over between two chromatids of homologous chromosomes. This will be of particular importance later in considering the behaviour and origin of complex and sex heterozygotes.

CHAPTER XI

THE THEORY OF MEIOSIS

Parasynapsis and Telosynapsis—Homology—Relation of Meiosis to Mitosis—The Precocity Theory.

> Make not impossible
> That which but seems unlike.
>
> SHAKESPEARE, *Measure for Measure*, Act V, Sc. (i).

1. HISTORICAL SKETCH

THE occurrence of meiosis as a concomitant of fertilisation was predicted on general grounds, and the universal verification of the prediction shows that meiosis is the same process in effect wherever it occurs. Step by step the unity of meiosis has been shown in all plants, animals and protista. It has been found, with a few exceptions, to be the same process in its course and in its results in all organisms. The first essential characteristic to be discovered, apart from the occurrence of two divisions, was that the reduction was brought about by the pairing of chromosomes and their segregation to opposite poles at the first division (Henking, 1891).

Two theories arose to explain how this pairing took place, both apparently supported by observation. The first assumed that the thick double threads seen at the prophase of meiosis (pachytene) correspond in every way—not merely physically, as they obviously do, but genetically—to the double threads seen at the prophase of mitosis (Häcker, 1892). On this view it was supposed that the chromosomes were united end to end in one unbroken thread, the so-called "continuous spireme." This thread broke up or "segmented" into the diploid number of chromosomes at mitosis and into the haploid number at meiosis. Thus the difference between meiosis and mitosis was simply a difference in "segmentation." This theory was plausible at the time because the chromosomes collapse on to the nearest rigid body—another chromosome or the nucleolus—with the least imperfection in treatment and thus give the appearance of continuity. Secondly, because the two stages when the double threads arise by pairing and when they develop by splitting into the metaphase bivalents are those when the threads are thinner than at the intervening pachytene and are in consequence more collapsed in treated material. Thirdly, because the very organisms in which these stages are the most completely obliterated are the ones in which the chromosomes at metaphase are attached end-to-end (following terminalisation) as this theory demands. Even, in some cases, with complete terminalisation association seems to begin at metaphase, owing probably to diakinesis repulsion being very strong (*cf.* Keuneke, 1923). For these reasons, in most organisms in which bivalent chromosomes have been found their development is still the subject of inference, and this theory of what became known as " telosynapsis " or end-to-end pairing, although now discarded by its former advocates, cannot even to-day be directly disproved in unfavourable material. There is now no reason to suppose that a " continuous spireme " is formed at meiosis in any organism, although it is reported in the oögonial mitoses of *Icerya purchasi*, an organism which is anomalous in other respects (*v.* Ch. XIII).

The first observations to show a continuous history of the structure of the chromosomes at meiosis were those of Winiwarter (1900) showing " parasynapsis " or side-by-side pairing of chromosomes. According to Winiwarter the double thread of the pachytene stage was the result of pairing of chromosomes in a single thread condition, and it gave rise to the metaphase bivalents by the later splitting of the double thread, to give interstitial as well as terminal association at metaphase. These observations were corroborated by the work of the Schreiners, Janssens, Grégoire and others, and are now taken to be the essential basis of meiotic behaviour in all groups of organisms.

It might be thought that these observations would have proved fatal to the theory of telosynapsis, but it was found possible to bring them into line with the theory by making certain additional assumptions. The occurrence of interstitial associations was held to be secondary, and either it was due to an attraction between the terminally paired chromosomes which opened a second split in each chromosome and gave the cross-shaped bivalent, with what we now recognise as an interstitial chiasma (Foot and Strobell, 1905), or it was due to the coiling of the chromosomes round one another (Farmer and Moore, 1905) to give the appearance described as " strepsitene."

Finally, the supposed pairing of the chromosomes at zygotene was taken to be merely a reassociation of the halves of single split chromosomes (Digby, 1919).

Before these arguments are dealt with, it is necessary to consider a special development of the theory of telosynapsis : its supposed accordance with the behaviour of the chromosomes forming rings in diploid plants (*v. Œnothera*). The development of these rings has until recently evaded observation for the reasons cited above, so that their interpretation has been a matter of inference. In order to understand the methods used the application of the theory of homology to chromosomes must first be appreciated.

Homology in geometry and chemistry is the correspondence of parts in relation to similar wholes. In biology the notion is restricted to a correspondence in ancestry, and this can be tested in the chromosomes by their pairing properties. Chromosomes which pair and pass to opposite poles at random with regard to other pairs must correspond in function, and, since the chromosomes are permanent in their properties, they must correspond in ancestry. With increasing accuracy of observation it has become possible to identify smaller and smaller units of homology. First, the chromosome came to be considered as made up of two segments each of which was homologous with a segment in another. This conclusion, reached by Belling (1927 *b et alibi*) from observations of interchange and reduplication heterozygotes, is equally clear from the observations of McClung and Seiler on fusion and fragmentation heterozygotes. Later it came to be considered as made up of very small segments each capable of showing its homology by its independent pairing properties (Newton and D., 1929 ; D., 1929 *c*). Finally, approaching the question from the genetical side, the individual genes in different species may be considered in regard to homology (as by Vavilov, Haldane, and Sturtevant) ; and at this point homology becomes chemical identity.

When the chromosomes were seen to pair at meiosis, it was found that only the chromosomes that corresponded in form associated in the pairs. The paired chromosomes must, therefore, on the theory of continuity be supposed to be related by inheritance (Montgomery, 1901). Moreover, since the members of a set were qualitatively different and *the pairs segregated at random*, the members of each pair must be held to correspond qualitatively if meiosis were to yield comparable gametes (Boveri). Thus evidence both of form and function showed the pairing and segregating chromosomes to be homologous, indeed, they must be homologous wherever they behave as units in segregation. Now in diploid ring-forming plants the chromosomes appear at meiosis in rings of four, six or larger numbers. Each chromosome is " paired " with two other chromosomes—one at each end—and only contributes to a viable haploid gamete when it has segregated from both of these. In these plants, therefore, *pairs of chromosomes do not segregate at random* and pairs of chromosomes therefore cannot be considered as units in regard to homology.

But the qualification was neglected for two reasons. First, it was considered axiomatic that chromosomes must behave as units (Gates, 1924). The theory of the individuality of the chromosome had emphasised their *permanence* at the expense of their equally obvious *variation*. Secondly, the appearance of the ring seemed almost a verification of prediction on the basis of telosynapsis: here was the continuous spireme incontestably present at metaphase, through a failure of segmentation—an unaccountable failure, to be sure, but a very credible one. This was accepted by most of the earlier workers on *Œnothera*. If then in ring-formation the chromosomes no longer seemed to behave as units, it was to be assumed that one of the associations was true pairing and therefore a criterion of homology, while the other was not, being merely a failure of segmentation (*cf.* Cleland, 1928; Gates, 1928). This conclusion of two kinds of pairing was improper because it was derived from contradictory premises, *viz.*, the assumption that pairing was determined by affinity of homologues and the assumption that pairing was derived from the failure of segmentation of the spireme in which homologous and non-homologous chromosomes alternated. The second assumption, plausible in itself, became, when associated with the first, the source of an absurd fallacy, and its genetical implications led to a variety of errors (*cf.* Whiting, 1923; D., 1929 *a*, 1931 *b*; Renner, 1929; Hoeppener and Renner, 1930).

Multiple-ring formation, as pointed out by Schwemmle (1924) and Kihara (1926), is found with parasynapsis, and the solution of the problem lies in the logical application of the theory of homology and the recognition that chromosomes need not behave as units.

It follows, therefore, that the theoretical unit of behaviour is a particle or chromomere, while effectively a series of particles or a whole chromosome may behave as a unit provided that the linear arrangement or " structure " of the series is the same in the two corresponding chromosomes, *i.e.*, when the organism is to that extent structurally homozygous. A part of a chromosome which behaves as a unit series is described as a *segment*. In segregation the chromosome acts as a mechanical unit, but it is not a genetical unit in hybrids. This is particularly clear in ring-forming hybrids, where effective segregation depends on disjunction of each chromosome from its partners at both ends. Each chromosome is then made up effectively of two segments homologous with segments in two other chromosomes.

These considerations have removed the objection to supposing that ring-forming plants are parasynaptic and have led to the present theory of ring-formation as determined by structural hybridity. Direct observation of every stage of meiosis in these plants has since verified this conclusion (Chs. V and XV).

The alleged observational evidence of telosynapsis has been contradicted by the closer investigation of the development of the paired chromosomes. The counting of the threads before and after zygotene pairing has shown that the single threads are indeed the whole somatic chromosomes (Fig. 20, Gelei, 1921; Janssens, 1924; Newton and D., 1929; Moffett, 1932 *b*). Observation of the later stages has been particularly stimulated by the theories and observations of Janssens (1909 and 1924), who showed that the points of association of chromosomes might be exchanges of partners between their chromatids, and that these chiasmata might be the result of genetic crossing-over (*cf.* Wenrich, Robertson, Belling and Newton). This work has made it possible to say that the coiled thread of strepsitene is a misnomer for the looped thread of diplotene, in which every loop is determined by two chiasmata. It has shown that all association between chromosomes after pachytene is essentially of this kind, and that the appearance of telosynapsis in plants as well as in animals is secondary and the result of terminalisation of the interstitial chiasmata.

Those who have held that chromosomes pair by reason of an affinity of homologous elements have not been able to treat this affinity otherwise than empirically or teleologically. O. Hertwig (1908) supposed that meiosis was determined by an abortion of the prophase of a normal mitosis, a view suggested by the intercalation of the diffuse stage in the prophase in many animals, but incompatible with more general observation, as Grégoire (1909) pointed out. Boveri (1909) and others supposed that the chromosomes pair with the object of reducing their numbers. Such statements are soporific: they give the impression, still a very general one, that there is no problem to solve.

Again it was often supposed that the pairing of the chromosomes was, in a sense, the culmination of the sexual process, and that it consisted essentially in the union of chromosomes from opposite parents. This was disproved, equally by the autosyndesis of chromosomes in polyploids, and by their pairing in certain parthenogenetic organisms where there was no sexual process to be brought to a culmination—where the chromosomes that pair were derived from the same parent and only separated from one another by one generation of mitoses (*cf.* Belar, 1923, and Ch. XV).

Now meiosis has always been recognised as a form—a complicated form—of mitosis, since, like mitosis, it effects the separation to pairs of daughter-nuclei of longitudinally split halves of chromosomes. The immediate problem of meiosis is therefore the problem of how it is related to mitosis and how it can have been derived from it. It will be seen that we now probably know enough to attempt to describe this relationship. The materials for induction consist in comparative observations, first, of meiosis and mitosis, secondly, of forms of meiosis in different species, and, thirdly, hybrids and mutants of the same species. The general morphological comparison of meiosis and mitosis will be made first, for it is on this that any general hypothesis must be founded, particular observations being used merely to test it.

2. THE RELATION OF MEIOSIS TO MITOSIS

(i) **The Essential Characteristics of Mitosis.** The beginning of prophase consists in a change in the chromosomes from a more dispersed to a less dispersed condition. At the moment this change takes place the chromosomes are already divided throughout their length, so that the two daughter threads are structurally free from one another. They remain lying side by side, however. This indicates that the two halves of each chromosome have a pairing attraction for one another and that this attraction is specific. They retain the attraction until they have been pulled apart at anaphase. Throughout the prophase the chromosomes contract longitudinally and the degree of contraction is a constant property of the organism as a whole, except in some Protozoa (*e.g.*, *Aggregata*, Dobell, 1925; Belar, 1926 *a*) where the degree of contraction and the duration of prophase are subject to correlated variation.

The behaviour of the spindle attachment during prophase is different from that of the rest of the chromosome. At early metaphase the two chromatids are held together closely at this point as though the spindle attachment were single; at anaphase it is manifestly double, and the two daughter attachments behave as though they repelled one another. This change can be most simply represented by supposing that the attachment divides at metaphase and pairs of attachments repel one another.

Summing up, therefore, four characteristics of mitosis may be noted :—

(i) The chromosomes divide during the resting stage.

(ii) The chromatids are attracted to one another in pairs during prophase. Only similar chromatids are attracted; the attraction is therefore specific and one-to-one.

(iii) The chromosomes contract during prophase to a uniform proportion of their length so as to give a uniform breadth.

(iv) The spindle attachment changes in character, probably by dividing, at metaphase, and this leads to orientation of the chromosome and separation of the chromatids.

It seems probable that mitosis must have developed these essential characters before meiosis developed from it, since they seem to be necessary conditions for the equal division of the chromosomes and separation of their halves (*v.* Ch. XVI).

(ii) **The Essential Characteristics of Meiosis** (*cf.* Ch. IV). *The Resting Stage.* In animals the prophase of meiosis is often preceded by a resting stage even more incomplete than is found between the rapid segmentation divisions in the egg. The identity of the chromosomes can be traced from the preceding division in Orthoptera (Wenrich, 1916), Hemiptera (Reuter, 1930), and Diptera (Metz and Nonidez, 1921, 1923)—where, in *Asilus*, the prophase pairing can be seen to continue the telophase " somatic " pairing directly.

Leptotene-Zygotene. When the chromosomes become visible after the resting stage as continuous threads each of them is single.* When they pair side by side they give a double thread, which resembles structurally the double thread at the prophase of mitosis. In polyploids, as well as in diploids, the chromosomes associate in pairs, never in higher numbers. The association may, therefore, be supposed to be determined by the same physiological conditions as at mitosis, *viz.*, an attraction of threads in pairs. It was earlier supposed (*v. supra*) that this double thread corresponded also genetically to that at mitosis—that it was indeed composed of two halves of a single chromosome—a view no longer entertained. The singleness of the leptotene thread is of the greatest significance, for it excludes the possibility that division of the chromosomes normally occurs before the resting stage (*v.* p. 47, *cf.* Hedayetullah, 1931).

In pairing, therefore, the chromosomes may be said to convert to a normal mitotic condition, an abnormal condition of singleness brought about by prophase anticipating their division. This assumption of precocity in the prophase agrees with the observation that prophase may begin before the nucleus has entered the resting stage. It implies an independence of chromosome changes and the division mechanism. This is justified, as will be seen, from observations of metaphase and later stages.

---

* Several observers consider that the leptotene thread is double. McClung (1927) and Robertson (1931 *a*) argue from the alleged doubleness of the chromosomes at telophase; this interpretation is invalid (Ch. II). Robertson also mentions that Bridges and Anderson (1925) have shown that the chromosomes were double before they *paired*. They actually showed the chromosomes to be double before they *separated*. Kaufmann (1931) states that the leptotene thread is divided, but gives no evidence for it. Since this stage is, in suitable material of plants and animals, the simplest and most unequivocal in the whole history of the chromosomes, and these observers have not relied on direct observation, their opinion cannot be accepted as evidence (*cf.* Plate III).

Pachytene-Diplotene. The leptotene chromosomes are single, the diplotene double. There is therefore no doubt that the chromosomes divide during pachytene.

As Roux pointed out (1883, *cf.* Reuter, 1930) we cannot expect the " division " of the chromosomes to take place instantaneously. The constituent particles (chromomeres) must first reproduce themselves and then the thread which they constitute must divide. There are several reasons for making this distinction between the particles and the thread. The most important is that the chromosome must be supposed to contain other materials than the genetically specific chromatin (Ch. X, p. 291).

But apart from this complex constitution we must expect two stages in the splitting of the chromosomes : first, a reproduction, secondly a fission. The first signs of the reproduction are probably visible at pachytene when the quadruple character of the thread becomes visible (Newton and D., 1929). The fission seems to occur at the end of pachytene. Can it be that it determines the falling apart of the pachytene thread to give the diplotene condition ? This would mean that a double or paired condition was the only stable one for chromosome threads at the prophase of meiosis, whether two or four are present, as indeed it is at mitosis, and that the delayed division at the prophase of meiosis was responsible for the changes in relationship at zygotene and diplotene which are characteristic of it.

In testing this view the behaviour of polyploids at pachytene is naturally of crucial importance because homologous threads are present in threes and fours instead of in twos. Their behaviour answers to expectation : whatever the number of homologous chromosomes present they always associate, at any one point, in pairs.

Diakinesis. At diakinesis all the chromosomes, both paired and unpaired, homologous and non-homologous, repel one another. The centre of repulsion is the spindle attachment. Its effect is only clearly visible as between the paired chromosomes, and is therefore not comparable with anything seen at mitosis. Its occurrence emphasises the character of the pairing of chromosomes at this stage. It no longer depends on an attraction of pairs of chromosomes, for these actually repel one another, but on an attraction of pairs of chromatids. The unit of attraction is again the mitotic one, the chromatid. Two chromosomes are held together because four chromatids associated in two pairs change partners at one or more chiasmata. Again the pairing is a symptom of the attraction properties of threads seen at mitosis.

The statement that the chromosomes remain paired at diakinesis and metaphase only by virtue of the formation of chiasmata is a description of what is observed in the most clearly understood cases; it is an assumption when applied universally. This assumption has been verified quantitatively by the observations described earlier and summarised in the next chapter. (It has been contested by O'Mara, 1931, *cf.* D. and Dark, 1932.)

Thus we see that during meiosis the quality of attraction (an attraction of threads in pairs) is constant and is the same as that at mitosis; the unit of attraction, on the other hand, changes, because the division of the unit takes place during the process, as it does not do in mitosis.

Metaphase-Anaphase.—At metaphase of meiosis the chromosomes show the universal property of linear contraction but carry it further than at mitosis, that is, they contract to between two-thirds and one-third of their mitotic length. The diameter of their chromatids is greater and their bulk is, as far as can be told, the same. The "mitotic constants," apart from bulk, are therefore transposed at meiosis.

At metaphase of meiosis the behaviour of the chromosomes differs in two respects from that at mitosis. First, the individual chromosomes do not orientate themselves to the spindle in the normal way. Pairs of chromosomes orientate themselves as pairs of chromatids do in mitosis and unpaired chromosomes show no orientation at all. Secondly, when paired they never divide by separation into two chromatids, and when unpaired they do so only *after* the ordinary separation of paired chromosomes. One of the chromosomes of a trivalent in *Hyacinthus*, or of a disproportionately small bivalent fragment in *Tradescantia*, will divide like an unpaired chromosome, after the bivalent division. This delay is not due to the greater resistance of the halves of a univalent to separation, for a short univalent always divides after a long bivalent and the time when univalents divide is fairly uniform for all of them irrespective of size in a given species, therefore it must be due to a difference in the inherent capacity for division. This conclusion is borne out by the observation that when the two chromatids of one member of a trivalent are drawn towards opposite poles at anaphase, they remain held together at the spindle attachment (Fig. 36, B_2). The correlation of lack of orientation and lack of capacity to divide can be understood on one assumption, *viz.*, that the spindle attachment which has been supposed to divide at metaphase in mitosis only divides after the separation of the bivalents in meiosis ; at early anaphase it is still effectively single. Hence bivalents will only divide into pairs of chromatids which will always remain together at the attachment. Hence also univalents will fail to orientate themselves normally to the spindle, not having the necessary bipolarity. And hence finally they will come to orientate themselves and divide at a regular interval after the bivalents, determined by the mechanical fact of division of the spindle attachment. This assumption agrees with genetical observation and with the terminalisation and chiasmatype theories, which demand that the identical chromatids should remain together at the spindle attachment, although nowhere else. It means, like the leptotene singleness of the chromosomes, that the division develops earlier in meiosis, relative to internal changes in the chromosomes, than at mitosis.

The Second Division. The occurrence of a second division often following the first without any resting stage is significant. Meiosis could never have had the effect of reduction without the prompt occurrence of a second division, for had the chromosomes divided during the resting stage numerical reduction would not have occurred. This suggests that the second division was directly

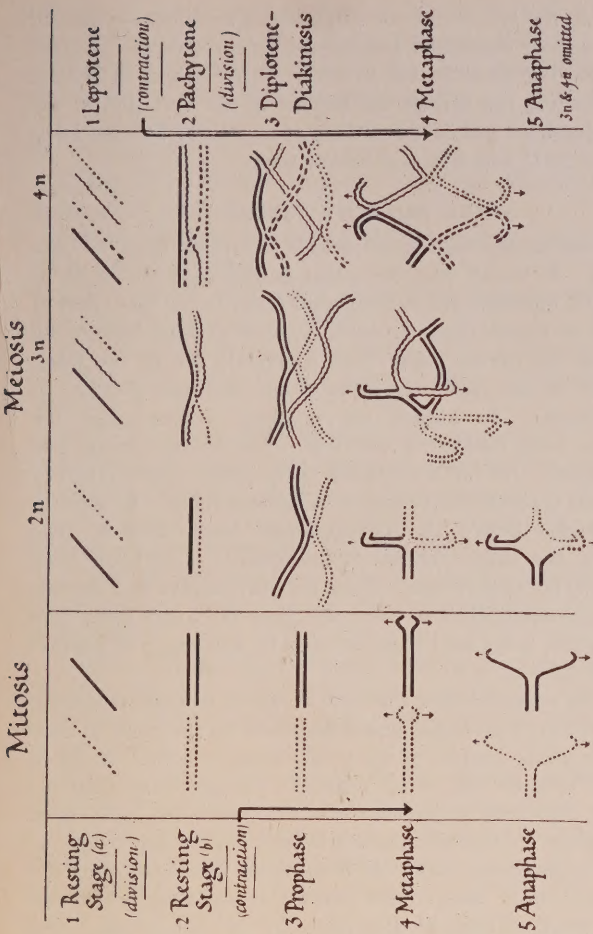

Mitosis
1 Resting Stage (a)
(division)
2 Resting Stage (b)
(contraction)
3 Prophase
4 Metaphase
5 Anaphase
Meiosis
2n
3n
4n
1 Leptotene
(contraction)
2 Pachytene
(division)
3 Diplotene-Diakinesis
4 Metaphase
5 Anaphase
3n & 4n omitted

FIG. 79.—Comparative diagram of the development of the homologous chromosomes in mitosis in diploids and in meiosis in diploids, autotriploids, and autotetraploids. Metaphase is shown at the same level in mitosis and meiosis; contraction, represented by an arrow, therefore begins in meiosis at a stage corresponding with resting stage in mitosis and lasts longer. Typical chiasma formation is shown giving a trivalent in the triploid and a quadrivalent in the tetraploid. The genetical interpretation follows the chiasma type hypothesis. The metaphase configurations are derived from the diplotene ones without terminalisation (except the trivalent, which does not correspond). Note that in all active stages until anaphase pairs of threads are united. (From D., 1931 *c*.)

stimulated by the exceptional doubleness of the chromosomes entering the resting nucleus, and that perhaps all nuclear division, apart from the first division of meiosis, is determined by division of the chromosomes.

Of course in the later evolution of meiosis a modified mechanism of division has been developed, independent of chromosome development in cause but co-ordinated in effect. This is seen in genetic variation affecting the spindle mechanism in the variation in the length of interphase and in aberrations of meiosis to be considered later (*cf.* Chs. XIII and XIV and Bleier, 1931).

3. THE PRECOCITY THEORY

The evidence of the relation of meiosis to mitosis has now been re-examined. It shows that the usual notion that the forces of attraction and repulsion are of a different order in the two types of division has no foundation. In both types of division there is an attraction of threads in pairs. The difference lies in the time-co-ordination of the beginning of prophase and the division of the chromosomes. In mitosis the prophase begins after the chromosomes have divided into halves. The halves attract one another in pairs. No further division takes place. The system of paired threads is stable until anaphase separates them. In meiosis, prophase begins before the chromosomes have divided. The attraction of the single threads is unsatisfied. They pair with homologues so far as they can. When they divide into four threads the temporary equilibrium is upset and they fall apart again into pairs of threads, being held together only by exchanges of partner amongst the pairs.

It might be expected that the time at which metaphase occurs, *i.e.*, the duration of prophase, was determined by the point in time at which prophase begins, or at which division occurs, or by a compromise between the two. With the changed time relationship of the beginning of prophase and the occurrence of division during prophase in meiosis, the contraction might last longer or metaphase might come earlier in relation to the division of the chromosomes. Both these results seem to be produced, so that the duration of prophase must be determined by the compromise. The chromosomes having begun to contract earlier in relation to division, the contraction continues later than in mitosis, for the chromosomes are shorter ; but not so late in relation to division, for metaphase is reached before the spindle attachment is divided. Pairs of chromatids act as units at the first division and their presence in pairs at the end of the division precipitates a second.

Summing up : The essential similarity of meiosis and mitosis is shown by the following common properties :

1. The division of the nucleus follows longitudinal division of the chromosomes.
2. The chromosomes contract longitudinally throughout the preparatory phase.
3. Half-chromosomes attract one another in pairs throughout the preparatory phase.
4. The spindle attachment of each chromosome divides a fixed time after the chromosome itself.

The essential difference between meiosis and mitosis is shown by the following properties of meiosis which distinguish it from mitosis :

1. The curtailed resting stage or *earlier* prophase.
2. The singleness of the leptotene chromosomes or their *later* division in relation to the beginning of prophase.
3. The greater contraction of the metaphase chromosomes or their *later* arrival at the metaphase condition.
4. The effective singleness of the spindle attachments of pairs of chromatids at metaphase or their *later* division in relation to metaphase.

Clearly all these differences can be represented as following from the first : the lateness of chromosome changes at meiosis relative to the division mechanism can be attributed to the original earliness of the division.

Meiosis differs from mitosis in the nucleus entering prophase before the chromosomes divide instead of after they divide.

That all the essential properties of meiosis should be explicable in terms of a simple physiological change is to be expected *a priori*. For the difference must be genetically determined, and it must have arisen as a single mutation, because no imperfect transition from mitosis to meiosis could have been inherited and adapted to its function. No transitional process could have been self-perpetuating. Meiosis must have arisen at a single step.

Critical tests of this hypothesis and of its numerous implications have already been described in their relation to other problems. It remains merely to classify them in relation to this one.

It is supposed that meiosis arose from mitosis and is distinguished from it by a single essential change : the prophase condensation or contraction begins before instead of after the chromosomes have divided. This precocity hypothesis has three corollaries of immediate interest, as follows :—

(*a*) *Physiological.* The special properties of the chromosomes at meiosis are conditioned not only by their own constitution but also by general developmental conditions affecting the time of division, as well as frequency of chiasma formation, and so forth.

(*b*) *Genetical.* The occurrence of meiosis instead of mitosis at one stage of the history of the nucleus is an act of differentiation, and, like all other acts of differentiation, it must be genetically determined. Conversely, the suppression of meiosis must also be genetically determined, and the frequency of pairing of chromosomes in hybrids cannot be taken as direct evidence of the closeness of their relationship unless genetic conditions affecting precocity, chiasma formation and behaviour and other conditions are known. The investigation of these genetical conditions may also throw light on related evolutionary problems (Ch. XVI).

(*c*) *Mechanical.* Comparison of mitosis and meiosis on the basis of the hypothesis shows the kinds of forces operating between chromatin structures in both types of division ; especially it shows that the forces of attraction are chemically specific while those of repulsion are non-specific.

These two latter corollaries of the hypothesis will now be considered.

CHAPTER XII

THE MECHANICS OF CHROMOSOME BEHAVIOUR

Types of Chiasmata—Terminalisation—The Conditions Affecting It—Terminal Affinity of Chromosomes—Chromosome Movements—Analysis of Attractions and Repulsions.

> Optime autem cedit inquisitio naturalis, quando physicum terminatur in mathematico.*
>
> Bacon, *Nov. Org. II.* 8.

1. THE CLASSIFICATION OF CHIASMATA

Primary association of chromosomes at meiosis may be defined in two ways. First, it is an association which influences, and, in bivalents, determines, the segregation of the associated chromosomes to opposite poles; this distinguishes it from "secondary pairing" (*v.* Ch. VIII). Secondly, it is an association in which the effective unit is not the chromosome but the chromatid. It depends on the attraction that corresponding parts of pairs of chromatids have for one another, and it is limited to pairs. The structure which makes this association of chromatids capable of holding together, not merely two chromosomes but an indefinitely large number, is the chiasma.

Reviewing the observations, earlier described, of meiosis in diploids, polyploids and structural hybrids, we notice that chiasmata seen at metaphase may be classified in the first place according to whether they are *interstitial* or *terminal*. An interstitial chiasma is always of one kind. The only conceivable complication of this form is that where two such chiasmata involving the six chromatids of three chromosomes might coincide. This has not been observed. The terminal chiasma, on the other hand, has various complications. Several such chiasmata may coincide, and we then have a *multiple* chiasma. Again a chiasma which is terminal for one chromosome may be interstitial for its partner, with a part of which it is homologous, and then we have a *lateral* chiasma. Lateral chiasmata are of two kinds: those which *must* be supposed to arise from terminalisation of a single chiasma (*i.e.*, a single cross-over on the chiasmatype hypothesis of several non-compensating chiasmata, and those which must be supposed to arise from two chiasmata which have been compensating (*v.* Ch. XI). The first gives a symmetrical configuration, the second an asymmetrical one.

---

* And inquiries into nature have the best result when they begin with physics and end in mathematics.

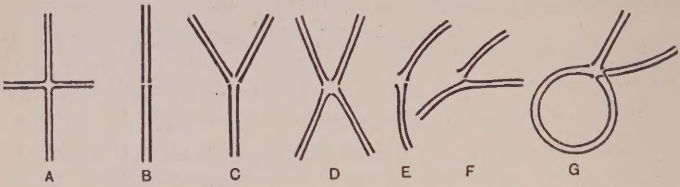


FIG. 80.—Diagram of chromatids showing different types of chiasma observed at metaphase and early stages. A, interstitial chiasma. B, terminal chiasma. C, triple (terminal) chiasma. D, quadruple chiasma. E, imperfect terminal chiasma. F, imperfect lateral chiasma (asymmetrical type—for symmetrical *cf.* Fig. 74 c_1). G, lateral-terminal chiasma, one chromosome having a reduplicated segment. (From D., 1931 *c*.)

Multiple combinations of chiasmata, arising presumably through pairing of reduplicated segments in the same chromosome, may include lateral chiasmata (Fig. 39).

When terminalisation is complete every chromosome end that is associated by a chiasma with another end remains so associated through diakinesis and metaphase until anaphase, so that the same proportion of ends of chromosomes is found associated at metaphase by terminal chiasmata in any organism as there were arms earlier associated by interstitial chiasmata. One change only may take place, and this in special circumstances, the breakage of the attachment between one pair of chromatids. Where four chromosomes are associated by a quadruple chiasma the double repulsion between them seems able to break one of the four chromatid associations, so that the cross-quadrivalent becomes a special kind of chain-quadrivalent (Fig. 35 IV, *c*). Where one chromosome is associated by a lateral chiasma with another the unequal strain on the two chromatids causes similar breakage of one attachment (Fig. 38). Either of these two events gives an *imperfect* chiasma (D., 1929 *c*).

2. TERMINALISATION

(i) **General Character of the Change.** Chiasmata are first seen through the opening of loops separating pairs of chromatids at diplotene. Their position cannot be accurately recorded at the very moment of origin, but nevertheless when the records of the earliest stages are compared with those of diakinesis and metaphase it is always found that they have changed in position. The change cannot be observed in living nuclei, but it is inferred from a comparison of records at the two stages in fixed preparations which show great constancy in the character of the change. This comparison reveals the conditions summarised earlier (Ch. IV) for the purpose of understanding the form of the metaphase bivalents, namely, the occurrence of a range of types of behaviour from those in which the change is scarcely detectable to those in which the form of the bivalent is entirely altered owing to complete "terminalisation" of chiasmata. The proportion of the total chiasmata that are terminal in any given type of chromosome or at any given stage is conveniently used as a *terminalisation coefficient* (D., 1931 *d*). These different kinds of behaviour now call for exact analysis to show the changes in number and position of chiasmata, *i.e.*, in the association of the chromatids, for several reasons. Observations of meiosis are usually confined to metaphase. An exact understanding of the kinds of change in bivalent structure which lead up to metaphase is necessary in interpreting these observations. Such an analysis is also necessary in deciding what forces hold the paired chromosomes together during and after the observed changes in their relationship, and what forces determine these changes. Further, the changes in number and position of chiasmata during prophase must be followed in order to know whether there is any possibility of exchanges in linear connection amongst the threads such as would determine genetic crossing-over (Ch. X). With the same end in view a record of the development of chiasmata is necessary in order that their number and position at the moment of origin (before they can be recorded) may be inferred. Finally, a comparison of analysis of hybrids with that of pure forms will throw light on the differences between chromosomes which constitute hybridity and will show the principles on which unsupported metaphase observations of hybrids should be interpreted.

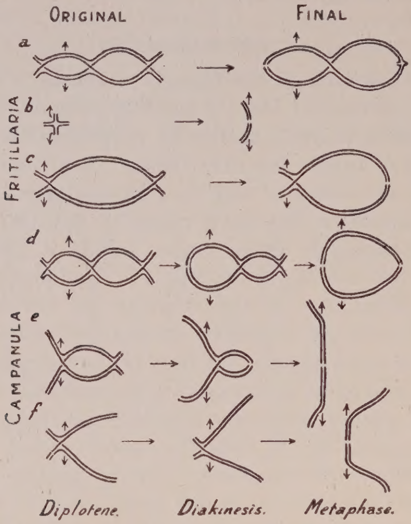


FIG. 81.—Diagram showing different types of terminalisation.
a, b, c : *Fritillaria* type with slight change of position and little or no reduction in number of chiasmata through fusion. *d, e, f* : *Campanula* type in which the movement is completed and results in terminalisation of all chiasmata. *Tulipa, Lilium* and *Rosa* are intermediate between the two. *b* shows that the same amount of movement as gives little change of appearance in the large chromosomes, in a fragment (of *Fritillaria imperialis*) gives complete terminalisation. c_1 a characteristic bivalent in *F. Meleagris* with localised chiasmata, shows that movement occurs in a distal chiasma although scarcely evident in the proximal one. *e, f,* show alternative behaviour to *d* where chiasmata are formed only on one side of the spindle attachment, but conditions are otherwise the same. This explains the origin of the two types of bivalent form in " type C " in *Phrynotettix* (Wenrich, 1916, *cf.* Fig. 75), and " type 7 " in *Circotettix* (Helwig, 1929).

Chiasmata must be supposed to arise interstitially, as exchanges of partner amongst chromatids, on four grounds: (i) a strictly terminal origin excludes the possibility that chiasmata arise always as exchanges of partner, and demands therefore a dual explanation of their origin; (ii) a terminal origin is incompatible with the chiasmatype theory, which supposes that chiasmata arise through crossing-over, and therefore interstitially; (iii) terminal chiasmata are found at late diplotene more frequently in small chromosomes (*e.g.*, fragments in *Fritillaria imperialis*) than in large ones in the same nucleus, and while it is intelligible that the conditions of terminalisation are different in small chromosomes it is contrary to observations of frequency to suppose that the conditions of origin are different (Ch. VI); (iv) the terminalisation coefficient of bivalents having different numbers of chiasmata at diplotene in *Tulipa* shows differences such as are accentuated later in the course

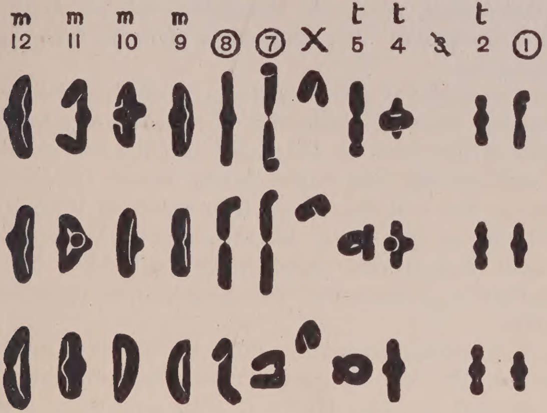


Fig. 82.—First metaphases in spermatocytes of three individuals of *Circotettix verruculatus*. X, the unpaired sex chromosome (*v*. Ch. XIV). m, chromosomes with median spindle attachments; t, with terminal. 1, 7, and 8, bivalents which are unequal in one or other animal. Note that the different forms of the bivalents are determined by the chance variations in the numbers and positions of their chiasmata. (From Helwig, 1929 *cf*. Table 50). × 1200.

of development, and may therefore be attributed to terminalisation (*v.* Table 49). Furthermore, the terminalisation coefficient is higher at the earliest recordable stage in organisms with complete terminalisation like *Campanula* than in those with slight terminalisation like *Tulipa* (*v.* Table 46 and Fig. 84).

Where several chiasmata are concerned the process has been most clearly shown in *Campanula* (D. and Gairdner, 1931) where terminalisation is complete, in *Rosa* (Erlanson, 1931), *Tulipa* (D. and Janaki-Ammal, 1932), and *Stenobothrus* (D. and Dark, 1932) where it is incomplete. The observations show the following rules of behaviour :—

(*a*) The movement is a movement away from the spindle attachment because when terminalisation is complete a proportion of metaphase chromosomes are rod-shaped having a terminal chiasma at one end, the rest ring-shaped having terminal chiasmata at both ends. The first type arises from diplotene bivalents with chiasmata all on one side of the attachment. The second type arises from those having chiasmata on both sides. Metaphase configurations of chromosomes with unequal arms agree with this assumption.

Thus in *Circotettix* (Helwig, *v.* Table 50) the short arm of the chromosome pair " type 7 " has a terminal chiasma proportionately less often than the long arm, and both arms have chiasmata proportionate in number to their length when compared with the pair " type 12." Since chiasmata are known to be formed in most organisms with a frequency proportionate to the length of the chromosome, this indicates that the terminal associations of each arm are derived from chiasmata in that arm, *i.e.*, that the chiasmata have remained in the arm in which they are formed and must therefore be moved away from the spindle attachment.

This conclusion is favoured by the behaviour in many organisms, especially those with small chromosomes. The paired chromosomes repel one another sharply at diakinesis to such an extent that all the chromosomes, paired and unpaired, appear to be distributed at random in the nucleus. Where interstitial chiasmata are still present (as in *Prunus*) it is then found that the repulsion is essentially between the spindle-attachments and the parts of the chromosomes between these and the first chiasma are therefore drawn out into a fine thread.

(*b*) All the chiasmata, both near to the attachment and further away, move at the same time towards the ends. The nearer ones do not catch up and meet the further ones. Thus the first change observed in terminalisation is that the distal chiasmata become terminal—without any reduction in the total number through a fusion taking place (*e.g.*, in *Fritillaria, Tulipa, Stenobothrus*). Moreover, if the proximal chiasmata caught up the distal ones they would in a proportion of cases cancel one another out, for the changes of partner at adjacent chiasmata can often be seen at anaphase to be reciprocal. The movement is not, therefore, merely an opening out of the attachment constriction loop at the expense

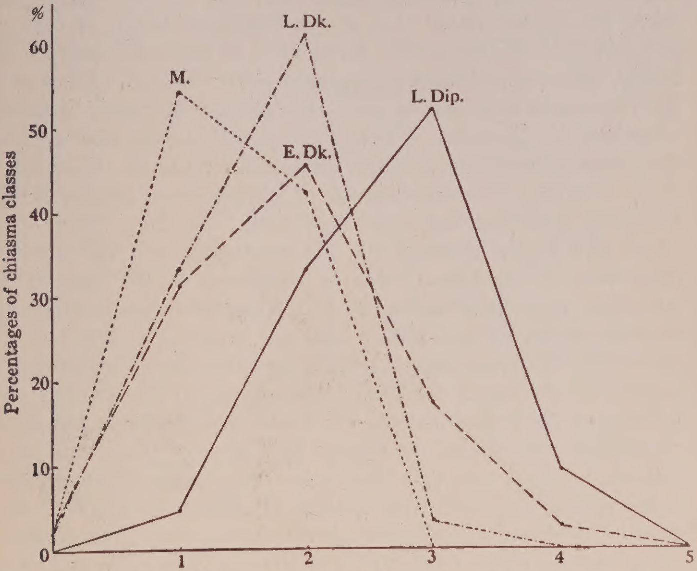


FIG. 83.—Percentage frequency polygons of numbers of chiasmata (abscissæ) in bivalents of *Rosa* " Orleans " at late diplotene, early diakinesis, late diakinesis, and metaphase of the first division in pollen mother-cells. (From Erlanson, 1931 *c*.)

of the distal loops, but a simultaneous movement of all chiasmata towards the ends and leading to fusion only at the ends.

(*c*) The chiasmata do not break in the course of terminalisation. This possibility, *i.e.*, that two of the four chromatids break and the four free ends rejoin in such a way that there is no longer an exchange of partners amongst the chromatids, was suggested before exact records were made (Janssens, 1924; D., 1929 *b*; Sax, 1930). It might be assumed either that all the chiasmata break, or that a proportion of the chiasmata, distributed at random, break; or, finally, that supernumerary chiasmata break, *i.e.*, so as to leave one chiasma in each pair of arms, thus giving association between all ends of chromosomes. The first and second of these assumptions is incompatible with the evidence summarised below that chiasmata alone condition the continuance of chromosome pairing from pachytene to metaphase in all organisms. The third possibility, which is a highly artificial one, is incompatible with the regular observation of a concentration of chiasmata at the ends at a late stage of terminalisation, and, in organisms with incomplete terminalisation, at metaphase. But the most conclusive test is afforded by the comparison of frequencies of bivalents with different numbers of chiasmata in certain *Tulipa* species (Table 47, Fig. 31) because in these no bivalents are found with just one terminal chiasma at metaphase. It follows that none of those with one chiasma can have earlier had two, since this chiasma is interstitial, *unless* breakage occurs. The numbers of chromosomes having one chiasma are found to correspond at the various stages, the changes being confined to the replacement of bivalents with three and four chiasmata by bivalents with two. Finally, in *Stenobothrus* and *Fritillaria*, where a high proportion of terminal chiasmata are found at metaphase, especially among the shorter chromosomes, the total number of chiasmata is unchanged between diplotene and metaphase. If breakage occurs in such organisms, each breakage of an interstitial chiasma must be accompanied by the making of a new terminal chiasma. In a word, it has become impossible to reconcile observation with the assumption of breakage (*cf.* Ch. X).

(ii) **The Origin of Terminal Chiasmata.** *Morphological Evidence.* It will be convenient at this point to summarise the evidence that terminal chiasmata correspond in development, in structure and in function to the interstitial chiasmata from which they are supposed to be derived. Evidence of structure will be considered first.

1. The terminal connection between pairs of chromosomes can always be seen to be double in favourable material, *i.e.*, to be a connection between pairs of chromatids not associated proximally.

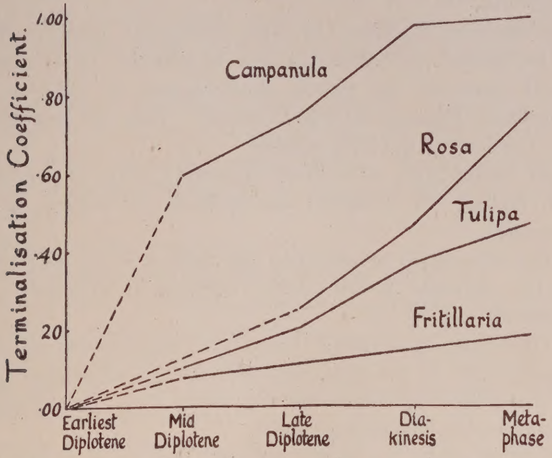


FIG. 84.—Graph showing the increase in the terminalisation coefficient from the earliest recordable stage (mid-diplotene) to metaphase in four types (*cf.* Tables 46 and 48). In all four the earliest values can be conveniently derived from a zero value at an earlier stage.

It is therefore a change of partner amongst chromatids (*Tulipa*, Newton and D., 1929; *Tradescantia*, D., 1929 *c*; *Prunus*, D., 1930 *a*; *Primula*, D., 1931 *a*; *Œnothera*, D., 1931 *d*, Catcheside, 1931; *Pyrus*, D. and Moffett, 1930).

2. The joint terminal connection between three and four chromosomes (triple and quadruple chiasma) can be seen similarly to be a change of partner amongst chromatids. The chromosomes are not associated as such, but by the property of pairing (and changing partner) possessed by their chromatids. By virtue of

this, one chromosome is never directly connected at the ends with more than two others (D., 1929 *c*, 1931 *a* ; Meurman, 1929 *a*).

3. Where the association between one pair of chromatids fails, the " imperfect chiasma " resulting gives less resistance to anaphase separation (D., 1929 *c*) and in a quadrivalent with a quadruple chiasma gives rise to a special type of configuration where the chromosomes are arranged in a line instead of in the cross (Fig. 35, IV, *c* and *d*).

Developmental Evidence. 1. The movement towards the end may be shown by comparing the frequencies of chiasmata in different parts of the paired chromosomes at different stages (*Phrynotettix, Primula, Matthiola, Rosa*). They are more frequent nearer the ends at the later stages.

2. At metaphase, interstitial chiasmata may be occasionally found instead of terminal associations (*Œnothera, Primula, Campanula*).

3. The proportion of terminal associations increases *pari passu* with the decrease in the total number of chiasmata (*Rosa, Campanula*).

4. The frequency of terminal metaphase associations of fragments is in proportion to the frequency of interstitial chiasmata found in large chromosomes, where the fragments therefore only develop one chiasma (*Fritillaria imperialis*).

5. Further, these fragments are only associated at one end, as they should be, having only one chiasma formed, although the larger chromosomes are associated at both ends, having several chiasmata formed (*Tradescantia, Fritillaria, Datura*, Blakeslee, 1931).

6. The terminal association of tetraploids and triploids does not consist in union of all homologous ends, but in a random assortment of possible associations of such homologous ends in every possible combination such as would be determined by chiasmata from randomly paired threads, as observed in a polyploid at zygotene (*Hyacinthus* and *Tulipa*), diplotene (*Primula, Campanula*) and metaphase (*Datura*).

7. Evidence from polyploids which agrees with the assumption that all chromosome association at meiosis is by chiasmata necessarily

implies as a corollary that a terminal association is a chiasma. This evidence is the degree of, and variation in, the frequency of multivalent association of chromosomes (sometimes of different lengths) in triploids and tetraploids already described (*Hyacinthus, Lilium tigrinum, Primula sinensis*).

8. Similarly, the association of chromosomes in hybrids whether terminal or interstitial agrees in its frequency and in its variation between different nuclei of the same individual and between the nuclei of different individuals, as is expected from the conditions, frequency and variation of chiasma formation (*Triticum, Crepis*, etc.).

(iii) **Conditions Affecting Terminalisation.** We now have information which shows in a general way the changes that may take place in the course of terminalisation. Numerous conditions have been found to influence these changes, of which the following are the chief :—

(*a*) Length of the chromosome.
(*b*) Original frequency and distribution of chiasmata.
(*c*) Agreement in the homologous linear sequence of the pair.
(*d*) Position of the spindle attachment.
(*e*) Rate of movement of the chiasmata.

The last two conditions have already been dealt with ; the first three will now be considered.

(*a*) *Length of Chromosome.* In *Nicandra* (Janaki-Ammal, 1932) terminalisation is complete in the shortest chromosome pair at late diplotene, and in the other short pairs at diakinesis, while in the longest chromosomes it is never complete. In *Fritillaria* (D., 1930 *c*) terminalisation is complete in the small fragments at late diplotene although it never has any effect in the long chromosomes, beyond leading to the movement of the distal interstitial chiasmata to the ends. This difference might be due in part to the chiasmata being formed nearer the ends in short chromosomes and in part to their being nearer the attachment constriction.

(*b*) *Number of Chiasmata.* Where the degree of terminalisation is low, as in *Lilium* (Belling, 1931) and *Tulipa* (D. and Janaki-Ammal, 1932), the number of chiasmata terminal, and even the proportion terminal, is higher the greater the number of chiasmata in the bivalent (Table 49). The *Tulipa* observations show that this is exclusively due to failure of chiasmata to be terminalised, in these organisms with low terminalisation, when they lie on one side only of the spindle attachment. It appears therefore that, other things being equal, movement is increased by the spindle attachment lying in a closed loop.

(*c*) *Chromosome Homology*. In certain organisms with more or less complete terminalisation interstitial chiasmata are occasionally found, sometimes very near the spindle attachment. When these were observed in a known structural hybrid (*Tradescantia*, D., 1929 *c*) the explanation suggested was that terminalisation was arrested by a change in the homology of the chromosomes. Thus, if two dissimilar chromosomes with a linear sequence *abcdef* and *abcxyz* with spindle attachments at *a* form a chiasma at *c*, terminalisation will be impossible without the particles *xyz* coming to pair with the particles *def* and leaving their identical partners. (This follows whichever theory of diplotene loop formation is adopted, *v.* Ch. X.) If we suppose that identical partners exert a certain attraction on one another and that dissimilar potential partners exert none (*i.e.*, that the specificity of chromosome attraction observed at zygotene still continues at diakinesis and metaphase), then it is possible that whatever forces determine terminalisation are unable to overcome the resistance to change from identical to non-identical partners, or rather to no partner at all, and in consequence movement of the chiasma is arrested. This conclusion has been borne out by the observation of exceptional interstitial chiasmata in *Œnothera* (D., 1931 *c*) between parts of chromosomes whose distal segments were dissimilar and were therefore, on this hypothesis, bound to prevent terminalisation. This and related observations on *Pisum* are closely concerned with the theory of genetical crossing-over and have been considered more fully in that connection (Ch. X and Fig. 103).

A variety of observations can probably be related with these on various grounds. Thus if an organism is known to be structurally hybrid and to have regular terminalisation as a rule, and it is found that an exceptional interstitial chiasma regularly occurs in a particular position in a particular bivalent, then, although it may not be possible as it was in *Œnothera* to show that there is a change of homology at the chiasma, the failure of terminalisation may reasonably be attributed to such a possible change. This is particularly clear in *Aucuba, Rosa* and *Datura.*

Another possibility is suggested by these observations. If two compensating chiasmata are arrested by a change of homology they will presumably cancel one another out or give an interlocking of chromatids such as is found in the anaphase separation of bivalents which have had such chiasmata at metaphase (Fig. 29). Such interlocking has not yet been observed, but it is possible that a great reduction in chiasma frequency without increase in the number of terminal chiasmata might be found in a hybrid on this account.

TABLE 45

Examples of Arrest of Terminalisation by Change of Homology

Established cases :	
Œnothera biennis . . .	D., 1931 *d*.
Pisum sativum . . .	E. R. Sansome, 1930.
Œnothera blandina (haploid) ..	Catcheside, 1932.
Rosa blanda . . .	Erlanson, 1931 *c*.
Possible cases :	
Tradescantia virginiana . .	D., 1929 *c* ; Koller, 1932 *c*.
Aucuba japonica . . .	Meurman, 1929 *a*.
Forficula sp. . . .	Payne, 1914.
(one chromosome pair shows subterminal chiasma at constant position).	
Datura hybrid . . .	Blakeslee and Bergner, 1930.
(bivalent with a " hump ").	
Œnothera (triploids) . .	Håkansson, 1930 *c*.
Campanula persicifolia . .	Gairdner and D., 1931.
Dahlia hybrid (6*x*) . .	Lawrence, 1931 *a*.
Cardamine pratensis . .	Lawrence, 1931 *b*.
Zea Mays, haploid gametophyte	Beadle, 1931.
(occasional pairs in polymitotic strain, Plate VII, Ch. XIII).	

TABLE 46

The Terminalisation Coefficient in Relation to Chiasma Frequency at Metaphase and at Diplotene

Species.	Diplotene.		Metaphase.	
	No. of Chiasmata.	Terminalisation Coefficient.	No. of Chiasmata.	Terminalisation Coefficient.
Lilium spp. (Belling, 1931) .	—	—	2·47	·16
Fritillaria imperialis				
"No. 13" (D., 1930 *c*, Figs. 5–8, *cf.* graph, Fig. 77) .	3·2	·078	3·2	·18
"No. 10"	4·6	·073	4·4	·32
Lathyrus odoratus (after Maeda, 1930 *a*, Fig. 1) . . .	—	—	2·57	·21
Pisum sativum (Pellew and E. R. Sansome, 1931) .	—	—	2·97	·46
Tulipa persica (D. and Janaki-Ammal, 1932) . . .	2·13	·105	1·95	·47
Triticum spp. (D., 1931 *d*) .	—	—	2·3	·65
Rosa blanda (Erlanson, 1931) .	1·94	·35	1·31	·69
Matthiola incana (Philp and Huskins, 1931)				
Long-chromosome race .	—	—	1·51	·87
Short-chromosome race .	—	—	1·54	·96
Primula sinensis (D., 1931) .	—	—	1·91	1·00
Campanula persicifolia (Gairdner and D., 1931) .	2·67	·60	1·90	1·00

TABLE 47

Changes in Chiasma Frequency during Terminalisation of Various Degrees

Percentages of Bivalents.	Numbers of Chiasmata.				
	0.	1.	2.	3.	4.
Tulipa persica					
Diplotene	—	12·5	64·1	23·3	—
Metaphase	—	15·8	72·5	11·7	—
Tulipa australis					
Diplotene	—	24·2	47·5	25·8	2·5
Diakinesis	—	28·3	71·6	—	—
Rosa "Orleans"					
Diplotene	0·0	4·8	33·3	52·4	9·5
Metaphase	2·9*	54·2	42·8	—	—
Campanula persicifolia					
Diplotene	—	1·5	45·3	42·2	11·0
Metaphase	—	10·5	89·5	—	—

* Difference from diplotene not significant.

TABLE 48

The Change in Chiasma Frequency from Diplotene to Metaphase with Partial and with Complete Terminalisation

	Mid-diplotene.	Late Diplotene.	Diakinesis.	Metaphase.
1. *Stenobothrus parallelus* *				
Total number of chiasmata per bivalent	2·05	2·07	2·12	2·09
Number of terminal chiasmata per bivalent	0·40	0·55	0·57	1·04
Terminalisation coefficient . .	0·19	0·26	0·27	0·50
2. *Tulipa persica*				
Total number of chiasmata per bivalent	2·13	2·04	2·00	1·95
Number of terminal chiasmata per bivalent	0·23	0·40	0·74	0·91
Terminalisation coefficient . .	0·11	0·20	0·37	0·47
3. *Rosa* " Orleans "				
Total number of chiasmata per bivalent	2·66	1·80	1·65	1·53
Number of terminal chiasmata per bivalent	0·65 †	0·46	0·77	1·16
Terminalisation coefficient . .	0·23	0·25	0·47	0·76
4. *Campanula persicifolia*				
Total number of chiasmata per bivalent	2·67	2·29	1·96	1·90
Number of terminal chiasmata per bivalent	1·60	1·70	1·93	1·90
Terminalisation coefficient . .	0.60	0·75	0·98	1·00

* Great size variation among the chromosomes.

† Observations of position at this stage uncertain.

TABLE 49

The Proportion of Terminal Chiasmata in Metaphase and Diakinesis Bivalents with Different Total Numbers of Chiasmata (Belling, 1931 *b* ; Pellew and E. R. Sansome, 1931 ; D. and Janaki-Ammal, 1932 ; Moffett, 1932 *a*).

No. of Chiasmata per bivalent.	Terminalisation Coefficient.							
	Lilium spp.	*Tulipa.*			*Pisum sativum.*	*Kniphofia.*		
		persica.	*australis.*	*stellata.*		*Leichtlinii.*	*Nelsoni.*	*Burchellii.*
1	0·00	0·00	0·00	0·17	(0·5)*	0·13	0·28	0·34
2	0·17	0·47	0·44	0·49	0·36	0·44	0·49	0·63
3	0·17	0·50	—	0·54	0·47	0·33	0·33	0·50
4	0·14	—	—	—	0·45	—	—	—
5	(0·20)*	—	—	—	0·40	—	—	—
Mean number . .	2·47	1·95	1·71	1·77	2·97	1·7	1·8	1·6
Mean number Terminal X^{ta} per bivalent . .	0·39	0·91	0·65	0·79	1·36	0·59	0·76	0·88
Mean coefficient .	0·16	0·47	0·38	0·45	0·46	0·35	0·41	0·55

* Too few observations to be significant.

TABLE 50

The Frequency of Terminal Chiasmata in Chromosome-Arms in *Circotettix verruculatus* (from Helwig, 1929, Plates 1–6, *cf.* Fig. 82), showing that it is proportionate to the length as is the frequency of interstitial chiasmata in *Hyacinthus* and *Vicia.*

Chromosome Pair.	No. of Bivalents.	No. of Chiasmata in Arms or Bivalents.				Total No. of Chiasmata.	No. of Terminal Chiasmata.	Terminalisation Coefficient.	Chiasma Frequency.
		0X.	*1X.*	$2X^{ta}$.	$3X^{ta}$.				
Type 7									
Long arm .	28	3	22	3	—	28	12	0·43	1·00
Short arm .	28	25	3	—	—	3	2	0·67	0·11
Both arms .	28	—	25	3	—	31	14	0·45	1·11
Type 12									
Both arms .	61	—	2	49	8	124	72	0·58	2·13

(iv) The Forces Effecting Chiasma Movements. Terminalisation must be regarded as the effect of unequal forces of repulsion acting between the pairs of paired chromatids on opposite sides of the chiasmata so that the association of the pair that repel one another more gains at the expense of the other and the chiasma moves along.

There are seven kinds of conditions on the two sides of a chiasma, five of them differential, according to whether the chromosomes are in closed loops or lie free (with open arms), and according to whether they have or have not the spindle attachment in the loops or arms. These show which differences are associated with movement and may therefore be attributed to differential repulsion, as follows :—

(i) Closed loops repel one another more than open arms : for distal chiasmata move towards the ends even though no other movement is detectable. And chiasmata in *Tulipa* move away from the spindle attachment when it is in a closed loop but not when it is an open arm (*i.e.*, when only single chiasmata are present).

(ii) Loops or arms, including the spindle attachment, repel one another more than others : for the spindle attachment loop is always the largest. But if the spindle attachment is in an open arm and on the other side of the chiasma is a closed loop the extra repulsion between the spindle attachments may not give equilibrium until the attachments are drawn closer by the chiasma moving nearer them.

From these two series of observations, it may be inferred that two kinds of repulsion occur between the chromosomes (paired chromatids) : First, a general repulsion between all parts of the chromosomes such as might be determined by a surface electrical charge ; this would be stronger between loops than between free arms, because their parts would be held closer together. Secondly, a localised repulsion between the spindle-attachments of the chromosomes. The first assumption is justified by the staining properties of the chromosomes, by the fact that unpaired chromosomes never touch one another in the nucleus, and by the known behaviour of ampholytes in solution. The second assumption is justified by the observed special state of tension found at diakinesis and metaphase at all terminal chiasmata and between the spindle attachment and the first interstitial chiasma wherever these are close together, as they regularly are in small chromosomes and in large chromosomes where the chiasmata are localised (Fig. 28).

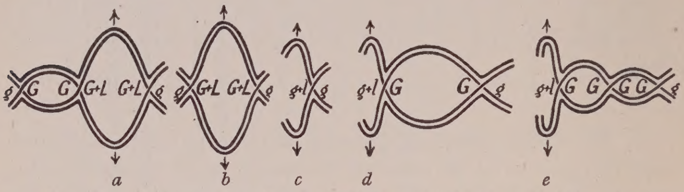


FIG. 85.—Diagram showing how differential forces will determine the movement of chiasmata. *G*, *g*, the generalised repulsions between all parts of all chromosomes. *L*, *l*, the localised repulsions between spindle attachments (marked by arrows). Capitals represent the forces within a closed loop, small letters between open arms. In all types *G* overcomes *g*. In *Tulipa* $g + l$ does not overcome *g*, but in *Campanula* it overcomes even *g*. In *Fritillaria* *G* may be greater than $g + l$.

These two assumptions explain the movements of chiasmata so far as they are yet known (D. and Dark, 1932). In organisms with the least degree of terminalisation, such as *Lilium*, *Hyacinthus*, *Fritillaria* and *Vicia*, the generalised repulsion alone is effective and no fusion of chiasmata seems to occur. In organisms with slightly more terminalisation such as *Stenobothrus* and *Tulipa* the spindle attachments are seen to repel one another and their loops become larger than others, but again little or no fusion of chiasmata occurs, and this repulsion even is scarcely effective to move chiasmata when the spindle attachment lies in an open arm. In organisms with still more terminalisation such as *Rosa* and *Matthiola* the spindle attachment loops expand considerably at the expense of the others, and most of the chiasmata are forced to the ends, where the supernumerary ones fuse. Finally, in organisms with complete terminalisation such as *Primula* and *Campanula* these changes are already well advanced at the stages of diplotene observed, and all the chiasmata, with rare exceptions, have reached the ends and fused before diakinesis. It can therefore be supposed that the generalised repulsion is a common property of all chromosomes after they have divided into chromatids and that the differences in degree of terminalisation observed in different organisms are due to differences in the degree of repulsion between spindle attachments.

There is one respect, however, in which observation and hypothesis are as yet indecisive. Where two loops of unequal size, neither of which includes the spindle attachment, lie next to one another, it might be supposed that equilibrium would be reached either by the absorption of the small by the large or by equalisation. The uniformity of the loops observed at diakinesis and metaphase in plants with numerous chiasmata and little movement (*e.g.*, *Vicia*, *Lathyrus*, *Hyacinthus*, *Lilium*, *cf.* Belling, 1931 *b*) may be put down to original interference between chiasmata, but more probably it is due to a movement of equalisation. Further study should make this point clear.

(v) The Relation of Terminalisation to Other Phenomena. The conclusions arrived at with regard to terminalisation are essential parts of the following arguments:

(*a*) Showing whether breakage of chiasmata occurs during prophase (*v*. Ch. X).

(*b*) Showing the forces of repulsion at work between the chromosomes during prophase (*v*. section 4).

(*c*) Showing the structural relationship of dissimilar chromosomes which are paired terminally at metaphase in complex heterozygotes and sex heterozygotes (Ch. XIV).

(*d*) Showing the inference to be drawn where these chromosomes are occasionally found with interstitial chiasmata at metaphase (*v. supra*).

3. THE THEORY OF THE TERMINAL CHIASMA

The evidence now available shows two rules with regard to the origin and persistence of chiasmata :

(i) All terminal associations at diakinesis and metaphase derived from prophase are chiasmata, *i.e.*, new associations are not made after diplotene. This is shown by developmental studies of terminalisation.

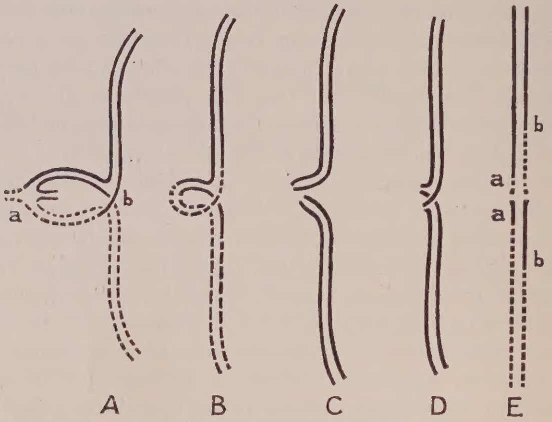


FIG. 86.—Diagram showing two possibilities of terminalisation of compensating chiasmata " a " and " b " (A, B and E showing genetic interpretation on chiasmatype hypothesis). B, first stage of terminalisation from A. C, the result if the chiasmata cancel one another out ; D and E, the result if the penultimate association replaces the distal one.

(ii) Conversely, prophase chiasmata when terminalised always persist as terminal associations at diakinesis and metaphase, *i.e.*, chiasmata are never broken, resolved or cancelled. This is shown by a comparison of fragment, trivalent and quadrivalent association.

with normal bivalent association. Exceptions to these rules will be considered later.

The conditions under which interstitial chiasmata are terminalised are essentially of three kinds, of which four examples may be given (illustrated diagrammatically in Fig. 87): (*a*) The chiasma is single, and there are two associations of chromatids. (*b*) There are two chiasmata, and therefore three associations of chromatids, but the third is a continuation of the first. The chiasmata may be said to be *compensating*. This does not mean, on the chiasmatype hypothesis, the assumptions of which are adopted in the diagram, that the same pair from the four chromatids have crossed over at the two chiasmata, but that *either* the same pair *or* a different pair have crossed over at the two chiasmata. (*c*) There are two non-compensating chiasmata: the second exchange does not restore the relationship found before. Necessarily, therefore, on the chiasmatype hypothesis one chromatid which has crossed over at the first also crosses over at the second chiasma. The chiasmata are also bound to be non-compensating where (as in (*d*)) a third chromosome associates at the second chiasma with one of the other two. All these types have been determined in organisms not having complete terminalisation, *e.g.*, compensating and non-compensating chiasmata in *Stenobothrus* (Janssens, 1924; Belar, 1929 *a*; D. and Dark, 1932), *Fritillaria* (Newton and D., 1930), *Pisum* (Pellew and Sansome, 1931), and *Kniphofia* (Moffett, 1932 *a*); and may be assumed to occur equally in diploid and polyploid organisms with complete terminalisation (*v.* Plate VI).

Now terminalisation of these different types introduces relationships between threads of a kind not paralleled at mitosis, and therefore having results not to be predicted on the basis of the theory that meiosis is a precocious mitosis. The maintenance of terminal association following the movement to the ends of chiasmata having all these different relationships leads to the following conclusions: (i) The proximal or penultimate association replaces the distal or ultimate one in terminalisation (Fig. 86 (*a*)) in every particle save the terminal one. (ii) Compensating chiasmata (Fig. 86 (*b*)) do not cancel one another out, but the penultimate association replaces the ultimate one. (iii) Non-compensating

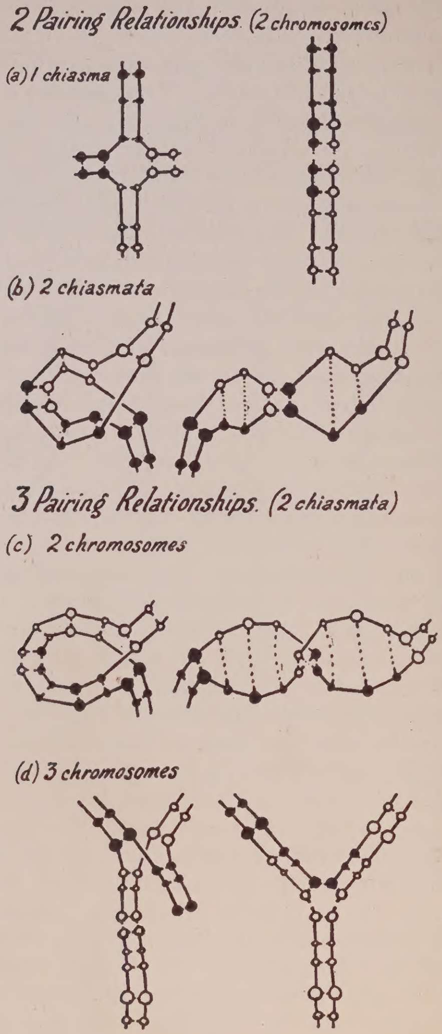

2 Pairing Relationships. (2 chromosomes)
(a) 1 chiasma
(b) 2 chiasmata
3 Pairing Relationships. (2 chiasmata)
(c) 2 chromosomes
(d) 3 chromosomes

Fig. 87.—Diagram to show how terminal affinity will preserve terminal association with terminalisation of chiasmata having different relationships. The genetic interpretation follows the chiasmatype hypothesis. Left, before fusion of chiasmata ; right, after fusion. If the end particles had not both lateral and terminal affinity the second type would give failure of pairing owing to its chiasmata being compensating. The dotted lines indicate the affinities that are satisfied after terminalisation.

chiasmata terminalise without replacement of the ultimate association. The penultimate association simply disappears.

These three unexpected properties can all be explained on a single assumption: the terminal particles have, unlike the intercalary particles, a double affinity, lateral and terminal; the latter is satisfied only on terminalisation. That terminal particles should inherently have a special affinity not found in intercalary

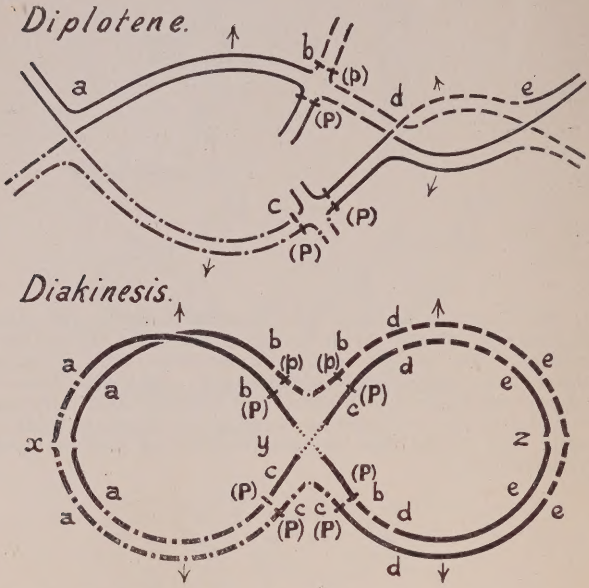


FIG. 88.—Diagram to show terminalisation in a quadrivalent giving a quadruple chiasma and the possibility of "double reduction" (or "equational exceptions") following crossing-over between chromatids (on the chiasmatype theory). a, b, c, d and e, diplotene chiasmata and points of crossing-over. x, y and z, terminal chiasmata. P and p, alternative factors in respect of which the organism is triplex (PPPp). Segregation will give double reduction in a proportion of cases yielding reduced nuclei of the constitution pp. Arrows show the positions of the attachment constriction (*v.* p. 280).

ones does not seem improbable on analogy with attraction based on chemical, electro-magnetic or surface tension phenomena, though we need not inquire for the moment which kind of attraction is here concerned.

The result of *terminal affinity* will be that when one thread displaces another from association with a third, *either* the end of the laterally displaced thread will retain its lateral association as a terminal one (as in case (*a*) with a single chiasma, or in case (*b*) where the displacing association is the same as the terminal one owing to the chiasmata being compensating) *or* the lateral association at the end of the displaced thread will be lost (as in cases (*c*) and (*d*) where the three associations are different owing to the chiasmata being non-compensating). The terminal association, therefore, cannot be eliminated by cancellation (as suggested earlier by the present writer, 1929 *c*) it can only be changed (as in (*b*)) to become the lateral one.

It remains to be said that the property of terminal affinity can only be supposed to develop *after* the beginning of diplotene, for, were the ends already attractive at this stage, terminal chiasmata would arise at every chromosome end immediately and as a matter of course. Actually, it is improbable that any chiasmata are terminal at the moment of origin, for the reasons given above.

Terminal affinity is exerted as a rule only when one lateral association is displaced by another in terminalisation. But if terminal affinity develops after diplotene the possibility arises of its being a secondary cause of pairing at diakinesis or metaphase. Exceptional cases of this have been found in the sex chromosomes of *Lygæus* (Wilson, 1905), the microchromosomes of *Anasa* (Wilson, 1905), and *Alydus* (Reuter, 1930). These chromosomes do not as a rule pair at the prophase of meiosis. In *Alydus* this is apparently because they have already divided at the pachytene stage when the paired chromosomes have not yet divided. The microchromosomes pair momentarily at metaphase and separate at anaphase. The sex chromosomes divide equationally at the first division and their daughter chromatids pair at the second prophase. In the anomalous meiosis of *Llaveia* a pair of autosomes behaves in the same way (Hughes-Schrader, 1931). In either case the pairing is *end-to-end*, and not side by side. It indicates a special capacity of attraction in the ends of the chromosomes such as that which is assumed to maintain the terminal chiasma. Probably the sex chromosomes which pair in this way are homologous for too short a length to permit the formation of a chiasma if they were to pair at pachytene, but retain minute homologous segments that are sufficient to exert a specific terminal affinity.

One series of observations shows the positive character and importance of the property of terminal affinity. In *Anemone baikaliana*, Moffett (1932 *b*) finds a mean chiasma frequency of 6·1 at diplotene, reduced to 2·5 at diakinesis and metaphase. Partial terminalisation occurs and seems to take the normal course at first, yet at the later stages no terminal chiasmata are found ; those that are seen earlier disappear. The chromosomes of this species, therefore, have no terminal affinity at diakinesis and metaphase. In this they are so far unique. But it will be seen that such a property is incompatible with pairing in an organism having complete terminalisation and the combination of the two properties may be the condition of genetically determined failure of pairing in some organisms, *e.g.*, " asynaptic " maize (Ch. XIII). It may also be the condition in *Aphis palmæ* where the chromosomes, paired terminally, separate at diakinesis in the oöcytes which are to give diploid parthenogenetic eggs, and a single mitotic division of the unpaired chromosomes follows (de Baehr, 1919 *a*, Ch. XV).

Summing-up. Observations of the conditions of formation of simple terminal chiasmata and multiple chiasmata and of momentary metaphase pairing point to the *ends* of chromatids having a special property of affinity not inherent in the *middles*. This property is conveniently expressed by saying that the end-particles have a special " terminal affinity " ; they have a double capacity of attraction at diakinesis and metaphase, lateral and terminal. The property of terminal attraction is perhaps a manifestation of the universal property of attraction by which chromatin particles come to arrange themselves permanently in linear order, an attraction which is only half satisfied in terminal particles, and its exceptional absence in *Anemone* and elsewhere may be a secondary modification.

4. THE ANALYSIS OF CHROMOSOME MOVEMENT

(i) The Problem. Between successive divisions the chromosomes undergo no movement, and they are therefore aptly described as passing through a resting stage. At division they undergo a series of co-ordinated movements. The internal changes undergone by chromosomes in linear contraction have been considered in relation to spiral structure and the theory of crossing-over. It remains to consider their relations with one another and with external agents.

The movements of the chromosomes during division may be supposed to be brought about either by movements of the medium in which they are lying or by forces of cohesion, or attraction, and repulsion to which they are subject. There is definite evidence, to be considered later, in favour of supposing that movements of the medium affect the chromosomes at late anaphase. It is also possible to suppose that movements of the medium assist the coming together of homologous parts of chromosomes at zygotene, particularly in the polarisation of the nucleus at this stage. But there is no evidence that can be brought nor inference that need be drawn in favour of such effects at any other stage. The problem is therefore how to describe movements and conditions of temporary equilibrium in terms of attraction and repulsion.

The units of behaviour seem to be of three kinds: (i) parts of chromosomes, in so far as they are capable of independent movement and specific reaction; (ii) chromosomes, acting as units owing to the cohesion of their parts in so far as they are moved either by the aggregate effect of their parts or by their spindle attachments; (iii) the poles of the spindle.

The effects of any forces acting on or between the chromosomes must be limited by spatial considerations. The limitation is complete in the resting stage; it restricts the chromosomes to the nucleus during prophase; and it restricts their spindle attachments to the spindle during metaphase and anaphase when it has bipolarity. It may be noted that, with these limitations on movement, equilibrium can be reached in the absence of any forces of attraction.

(ii) The Method. New observations may now be used for the study of chromosome mechanics of a much more decisive character than those hitherto available (*cf.* McClung, 1932), either from experiment or natural observation. These throw light on the mechanism of chromosome movement, not only at metaphase and anaphase, but during the prophase stages of mitosis and meiosis. They fall under the following heads :—

1. Comparison of the prophase of mitosis with prophase of meiosis in diploids and polyploids up to diplotene (the basis of the precocity theory).

2. Comparison of the behaviour of chiasmata with various degrees of terminalisation.

3. Comparison of the shapes of all chromosome configurations at metaphase and anaphase of meiosis as affected by the numbers and distribution of chiasmata.

4. Comparison of the orientation and separation of bivalents on the spindle (*a*) with that of trivalents and quadrivalents in polyploids, (*b*) with that of chromosomes in chains and rings of various sizes in interchange heterozygotes (lagging, non-disjunction, etc.).

5. Comparison of behaviour of univalents with that of bivalents and of mitotic chromosomes.

6. Comparison of the distribution of bivalents on the equator of the spindle in diploids and in polyploids at meiosis with that of simple chromosomes at mitosis (somatic and secondary pairing).

7. Comparison of changes in the living spindle at anaphase in isotonic and hypertonic solutions (Belar, 1927, 1929, *a* and *b*).

(iii) **Forces at Prophase.** During prophase of meiosis, as has been seen in considering the precocity theory, uniform conditions govern the principal changes, and these are the same as those governing behaviour at mitosis, *viz.*: (*a*) an attraction between pairs of chromomeres which is specific and yields a condition of paired chromosomes, before division, or chromatids after division ; (*b*) a repulsion between different paired chromatids, which prevents them ever touching, and is non-specific.

The attraction is probably completely effective and the slight separation observed between pairs of chromatids (*e.g.*, at diplotene in Orthoptera) is in that case due to contraction in fixing. The attraction shows itself in one defined movement, the pairing at zygotene. The repulsion shows itself also in one defined movement, the opening of the diplotene loops.

Apart from these two movements confined to meiosis the relation of the chromosomes to one another is in equilibrium until the diplotene loops are formed. At this stage another change begins to occur, the movement of chiasmata, which may be described as the result, first, of the differential effect of the repulsion between pairs of paired chromatids, owing to some being held together in closed loops and others in free arms ; and, secondly, of the special repulsion of the spindle attachments. This is a new force, which never makes itself felt in the prophase of mitosis, and only in the prophase of meiosis in organisms with strong terminalisation. It might be thought that these repulsions were specific, since they are clearest between corresponding spindle attachments and between corresponding parts of chromosomes. But all the attachments, associated and non-associated, must be supposed to repel one another, in view of the distribution of the bivalents in the nucleus and in view of the equally clear repulsion of the dissimilar chromosomes in the multiple rings of diploid interchange heterozygotes. The fact that the chromosomes lie more on the periphery at diakinesis where they are small and not very numerous gives an appearance of unevenness which is deceptive ; they are distributed at the greatest distances apart compatible with evenness.

(iv) Forces at Metaphase. At metaphase in mitosis the spindle attachments of the separate chromosomes lie so that the two chromatids are there in the axis of the spindle, while in meiosis the two spindle attachments of the paired chromosomes assume the same polarity, although they are widely separated. Univalent chromosomes at meiosis do not at first show this polarity, although they later develop it. Apparently, therefore, two spindle attachments of a metaphase bivalent have the same properties in relation to the spindle as one has either in mitosis or at a slightly later stage in meiosis. The conclusion is obvious that the pair of chromatids which has a double or at least bipolar spindle attachment at mitosis has not reached this stage of development at the same phase of meiosis, but arrives at it just a little later by division. This is borne out by the sudden change in the behaviour of univalents in the course of anaphase.

The axial orientation and repulsion of the spindle attachments found at metaphase in meiosis and at the beginning of anaphase in mitosis is correlated with another directional difference. The spindle attachments of unconnected chromosomes or of chromosomes connected by intervening chromosomes and at the same level in the spindle still repel one another, but much less strongly. Repulsion therefore acts differentially in the spindle in regard to direction, and associated chromosomes will reduce the potential energy of the system by orientating themselves in that axis in which the repulsion is strongest. Further, where four chromosomes are associated the pairs of spindle attachments which are nearest one another orientate themselves axially rather than the more remote pairs (*e.g.*, in the ring-of-four in an interchange heterozygote in *Trimerotropis citrina ;* Carothers, 1931). This proves that the repulsion is less effective with increased distance. At the same time as the attachments arrange themselves axially they also arrange themselves equatorially, *i.e.*, at an equal distance from the poles, and reach equilibrium in this position. This means that the poles equally repel the chromosomes, for attraction would not produce an equilibrium. If the repulsion is electrical, as Kuwada and others suppose, the two poles and the chromosomes must be of the same sign.

The third point to be noticed about the distribution of the chromosomes at metaphase (both of mitosis and meiosis) is that it is even on the equator of the spindle just as it was even in the diakinesis nucleus, and similarly on account of the repulsion between the attachments of the separate chromosomes. Again the equilibrium position is more peripheral when the number of chromosomes is small, and less so when the number is greater ; whence a difference between meiosis and mitosis in the same organism ; whence also the more peripheral distribution of the chromosomes at mitosis in Orthoptera with few chromosomes than in those with more chromosomes. Apart from the effect of increased number in increasing the repulsions between the chromosomes, there are probably differences between organisms in the relative importance of this force. The *bodies* of the chromosomes themselves must also contribute to their repulsion for one another because, at meiosis when the rounded chromosomes move most freely in the cytoplasm, the larger chromosomes usually lie on the periphery, therefore while the spindle attachments are confined to the spindle the bodies of the chromosomes are spread out to the utmost. The equilibrium position reached at metaphase may therefore be described as the result of the combination of three kinds of repulsion acting on bodies in the confined space of the spindle.

Kuwada and his associates (1929) have compared the distribution of the chromosomes on the plate with the arrangements obtained in a magnetic field ; they used magnetised needles in floating corks. Their observations make it probable that the repulsions acting between chromosomes are nearly equal but are modified by size. This conclusion agrees with that obtained here by considering the phenomenon developmentally.

But the methods of Kuwada cannot be applied in greater detail on account of an essential objection. He considers the two poles of each chromosome as attracted to the opposite poles. This could not give an equilibrium position in the middle of the plate and could not possibly be applied to the consideration of multivalents and multiple rings. The same equilibrium distribution can, on the other hand, be accounted for on the present hypothesis, by the assumption of repulsions between all centres, provided that the chromosomes are held within the spindle by a crudely structural limitation to movement.

Kuwada's conclusions require modification in another way. Secondary pairing has been entirely neglected, although striking examples of it are afforded in the work discussed (*e.g.*, Hirayanagi on *Vitis*, $n = 19$). Evidently secondary and somatic pairing are due to a force of attraction which is specific. But it is so much slighter than the other forces acting on the chromosomes that it only succeeds in modifying the equilibrium position produced by these other forces—making it no longer comparable with that given by floating magnets.

The behaviour of chromosomes associated in chains and rings of four, six and larger numbers by terminal chiasmata is significant. On account of their simple structure these can readily be compared in different organisms. First it is found that the relationship of the chromosomes is indifferent to their orientation and distribution. A ring of four chromosomes behaves with similar variation in diploid

Campanula and in tetraploid *Primula*. The repulsion of the spindle attachments is therefore, as expected, non-specific. Secondly, it is found that the chromosomes are only arranged in one straight chain in the axis of the spindle when the chromosomes are very small in relation to the spindle (*e.g.*, in *Prunus* and *Pyrus*). Where they are larger the occurrence of even three in an axial chain is exceptional; that is, the chain is usually zigzag and disjunctional (*e.g.*, in *Primula* and *Œnothera*). Thirdly, it is found that the exceptions to the regular zigzag disposition are no more frequent in a ring of 12 or 14 than in a ring of 4 or 6 (Gairdner and D., 1932).

These last considerations may be taken to show that the orientation of the chromosomes is determined only when they lie in the neighbourhood of the equator. In this way the disjunctional orientation in the ring will begin in that part which happens first to lie in the equatorial zone. Then the chance of the orientation beginning independently, and leading to non-disjunction, if the systems of orientation meeting do not *agree*, will be as great in a small ring as in a large one. They also show that one chromosome affects its immediate neighbours strongly, but its more remote associates negligibly; this agrees with the repulsion being electrical or magnetic.

(v) **Forces at Anaphase.** After diakinesis the repulsions between all the chromosomes weaken, so that the whole body come closer together. This is "pro-metaphase." It may be that the weakening occurs when the chromosomes change from being electro-negative within the nuclear membrane to electro-positive in the spindle, a change inferred by Kuwada and Sugimoto (1928) from staining experiments. During metaphase the repulsions recover their force again, and there is no sudden change between metaphase and anaphase—as there is in mitosis. The chromosomes gradually separate, and in this movement give every appearance of continuing the effect of the repulsion of the paired attachments. The change is of the same character in mitosis and meiosis, a separation of chromatids whose attraction has until this point been insuperable. Belar has described the change as "autonomous" on the part of the chromosomes, since external agents cannot be connected with it. This is probably sufficient in describing mitosis: the division of the spindle attachment determines the separation of the chromatids. But it is more satisfactory in meiosis to describe it as a changing condition of equilibrium of the repulsion between the paired spindle attachments, on the one hand, and between each spindle attachment and its pole, on the other; the first repulsion increases as compared with the second, and equilibrium is maintained by the distance between the spindle attachments gradually increasing. This account agrees with the theory of spindle-attachment behaviour and properties described above.

When at mid-anaphase the chromosomes have separated a short way the body of the spindle lying between them is broad. This part of the spindle then narrows and stretches axially without changing its bulk. The change naturally pushes the chromosomes and the poles of the spindle apart, so that all the later anaphase movement can be represented as due to a change in the shape of the spindle and as external to the chromosomes. This movement is undergone by undivided univalents which do not move to the poles of themselves, as is often supposed. That this change was really active on the part of the spindle Belar argued from the effect of dehydration on it. The stretching was then so exaggerated that the shrunk cytoplasm would bend the narrow spindle back on itself. It is similarly possible to argue the special action of the spindle, apart from any effect of repulsion of the chromosomes, in genetically abnormal plants, such as *Kniphofia*; there the chromosomes separate, but anaphase is never completed and cell walls are not formed. The chromosomes play their part but the spindle fails.

Thus it is possible to suppose that anaphase movement is determined by the gradual waning of the repulsion of the poles on the spindle attachments of the chromosomes. The repulsions of the paired spindle attachments for one another then draw the chromatids or chromosomes belonging to them towards the pole with a force which diminishes with the distance apart, so that, as in mitosis, it is unequal to completing the movement. The middle part of the spindle then stretches and carries the chromosomes the full distance. Unpaired chromosomes which have lagged at meiosis are not carried to the poles if they lag too long, but owing to the slight pause between the two movements they frequently catch up.

The separation is assisted at mitosis, particularly where the chromosomes are very long, by a third factor, a further linear contraction of the chromosomes at late anaphase (in *Tradescantia* and *Aggregata*), but this contraction probably plays no part in meiosis.

(vi) **Classification of Forces.** The present outline of the evidence for different kinds of forces acting on chromosomes at mitosis and meiosis, if it does not provide the basis for a unified explanation of their mechanism and of the detailed relations between the two kinds of nuclear division, at least shows a part of the essential evidence for any later synthesis of this kind.

Meanwhile, it is of interest to consider the various forces whose action has been separately detected. They may be classified according to their origins and effects in the following way :—

A. *Attractions : all Chemically Specific,*

1. Between identical pairs of chromomeres and hence chromatids at prophase of mitosis and meiosis ; responsible for zygotene pairing.
2. Between homologous pairs of ends of chromatids in the terminal pairing of certain chromosomes at metaphase in Hemiptera ; responsible for the retention of the terminal chiasma ; probably a special case of (1).
3. Between homologous parts of chromosomes (when (1) is satisfied) responsible for somatic pairing and secondary pairing. This is always slighter than (4) and merely modifies the equilibrium position produced by (4), (5) and (6) when controlled by (8) at metaphase.

B. *Repulsions : all non-specific, probably by electrical charges.*

4. Between chromosomes consisting of paired chromatids
    - (*a*) at prophase and metaphase in mitosis ;
    - (*b*) from diplotene to metaphase in meiosis ; responsible for the opening of diplotene loops.
5. Between spindle attachments of paired and unpaired chromosomes : affects the distribution of (1) by terminalisation and overcomes it in the anaphase separation in mitosis and meiosis. (Assuming division of the spindle attachment at metaphase in mitosis and later in meiosis.)

6. Between poles and spindle attachments ; in equilibrium with one another at metaphase of mitosis and also with (5) at metaphase of meiosis until overcome by it at anaphase.

C. *External or Structural Conditions of Equilibrium and Movement.*

7. The nuclear membrane retains the chromosomes within a fixed space during prophase.
8. The spindle retains the spindle attachments within a fixed space during metaphase and anaphase.
9. The middle part of the spindle expands, forcing the chromosomes apart at late anaphase.
10. The spindle attachment does not divide until some time after the rest of the chromosome, so that chromatids are held together at this point by the internal cohesion of the spindle attachment. Division of the spindle attachment determines the sudden separation of chromatids of chromosomes at mitosis and at the second division, and of lagging univalents at the first division, but is unconcerned with the gradual separation of bivalents.

The combination of these conditions produces stable *equilibrium* throughout prophase and at metaphase of mitosis, and at the pachytene, diakinesis and metaphase of meiosis. It produces *movement* or change of equilibrium at anaphase and just before metaphase in mitosis and meiosis, and at zygotene and diplotene as well as in meiosis.

This seems to be as far as analysis will carry us at the present moment. Just as in regard to crossing-over we are satisfied (in spite of over-eager critics) to show when and where it occurs before we bother ourselves as to how it occurs, so in regard to the mechanics of mitosis and meiosis we can accept the forces acting on chromosomes as empirical " attractions " or " repulsions," making sure of their consistent action before we try to analyse them any further. " I do not anywhere take on me to define the kind or manner of any action, the causes or physical reasons thereof, or attribute forces in a true and physical sense to certain centres, when I speak of them as attracting, or endued with attractive powers." Thus the author of the law of gravity : need we be more confident ?

CHAPTER XIII

ABNORMALITIES OF MEIOSIS

Genetical Control of Chromosome Pairing—Abnormal Division, its Causes and Results—Polyploid Gametes—Meiosis in Haploids—Time Abnormalities—Polymitosis—Abnormal Meiosis : Rosa, the Coccidæ.

1. GENETICALLY DETERMINED FAILURE OF PAIRING

(i) **Classification.** According to the precocity hypothesis and the morphological observations on which it rests, the pairing of chromosomes at meiosis depends on a primary difference from mitosis, which is normally followed by a series of secondary differences. Any one of these may be liable to error in a given organism, for one of several reasons.

Dissimilarity of structure and unevenness of number reduces the length of chromosomes which can be paired at pachytene, and hence the amount of chiasma formation and metaphase pairing. But apart from this hybridity, genetical conditions can be shown to control the pairing of chromosomes. These can be classified according as they affect the original pairing of the chromosomes at pachytene, or the retention of this pairing by chiasma formation at diplotene. In terms of the precocity theory, the first should mean postponing the prophase, or hastening the development of the chromosomes. The evidence for this consists in the chromosomes being less contracted at metaphase than they normally would be (in *Matthiola*) or in the division occurring abnormally early or late (in *Ochna*, etc.). These abnormalities can only express themselves through reduction of chiasma formation. Where therefore the failure is directly due to failure of chiasmata, this can only be inferred from the absence of special symptoms of lack of precocity. The characteristics of failure of pairing owing to failure of chiasmata are observed in both classes—a unimodal variation in frequency of pairs under constant conditions. The genetic control may be inferred in a variety of ways, as will be seen.

The following classification shows the conditions under which chromosomes fail to pair.

TABLE 51

Conditions of Failure of Pairing

Immediate Condition.	Prior Condition.	Occurrence.
1. Lack of precocity of prophase.	Genetic-environmental reaction.	(*a*) Parthenogenesis of certain types (Ch. XV). (*b*) *Matthiola*, etc. (*v. infra*).
2. Reduction of pachytene pairing.	(i) Hybridity.	(*a*) Numerical hybrids. (*b*) Structural hybrids (Chs. V and XIV).
	(ii) Fragmentation.	Organisms with new chromosomes shorter than those in the regular complement (Ch. V).
	(iii) Genetic-chromosome reaction.	Organisms with differential precocity of particular chromosomes (*v. infra*).
3. Reduction of chiasma frequency per unit of length paired.	Genetic-chromosome reaction.	Many mutant and segregated types (*v. infra*).
4. Lack of terminal affinity.	Genetic-chromosome reaction.	Mutant types (? asynaptic *Zea* and some parthenogenetic organisms, *v. infra* and Chs. XII and XIV).

(ii) Failure through Lack of Precocity of the Division. 1. *Matthiola incana* (Lesley and Frost, 1927; Philp and Huskins, 1931). A recessive factor determines the lack of contraction in the chromosomes at metaphase of the first division of meiosis. They are intermediate in length between the mitotic chromosomes and the normal meiotic chromosomes. Since this reduced contraction (unlike the examples quoted in Ch. III) occurs at no other stage, it must be supposed to follow special conditions in the prophase of meiosis which might take two possible forms: a slower contraction or a shorter period of contraction. The latter is presumed, since on the precocity theory it enables one to predict a reduction of pairing which is actually found to be characteristic of this strain (*cf.* Hollingshead, 1932, on *Triticum vulgare,* and Figs. 89 and 90).

2. *Chrysanthemum* (Shimotomai, 1931 *b*). A similar reduced contraction occurred in small nuclei produced by irregular premeiotic divisions (Ch. III).

3. *Ascaris megalocephala bivalens* (Geinitz, 1915). In one individual there was failure of pairing of the chromosomes at the first metaphase, and they were of abnormally reduced contraction. The second division was irregular in consequence.

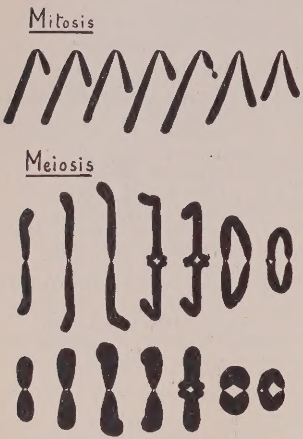


FIG. 89.—Diagram showing the metaphase chromosomes of *Matthiola* at mitosis, as they are in all forms, and at meiosis in the forms with long and with short chromosomes at this stage.

4. Many organisms with cyclical and facultative parthenogenesis produce unreduced egg-cells through failure of pachytene pairing. They probably do so by abolishing the precocity of the prophase. Thus, in parthenogenetic oöcytes of *Phylloxera* (Morgan, 1915), the characteristic contraction stage, probably associated with zygotene, is not found (*v.* Ch. XV).

5. *Allium odorum* (Modilewski, 1930). Some embryo-sac mother-cells have 16 pairs, others 32 univalents. This special susceptibility to environmental or developmental changes must be regarded as a genetic property like that of cyclical parthenogenesis.

6. Similarly in varieties of *Saccharum officinarum* (Bremer, 1929), and in *Kniphofia,* a variable genetic-environmental reaction is found to govern chromosome pairing. In different pollen mother-cells in *Saccharum,* 40 bivalents, 80 univalents or intermediate numbers are found. This might equally be due to genetic variation in chiasma formation.

A second kind of evidence of the effect of precocity on the pairing of chromosomes is provided by the frequent association of time irregularities with irregularity of pairing and segregation where variation occurs in the individual, and is therefore to this extent environmentally conditioned. It is to be expected on the precocity theory that two kinds of change would lead to failure of pairing : the too-early division of the chromosomes and the too-late beginning of the prophase. Since, according to the hypothesis, both of these affect the time of metaphase, both earliness and lateness should be associated with abnormality in the course of meiosis.

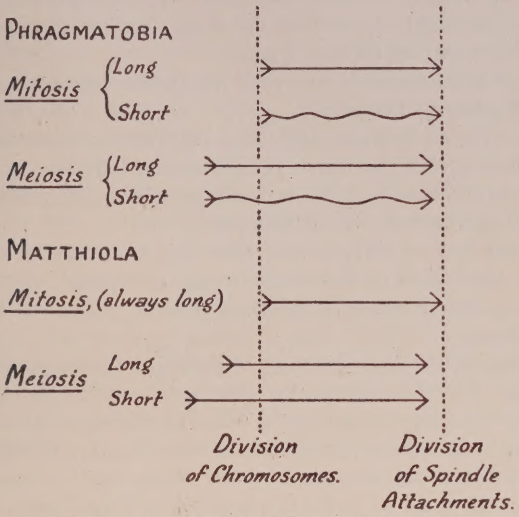

PHRAGMATOBIA
Mitosis
Long
Short
Meiosis
Long
Short
MATTHIOLA
Mitosis, (always long)
Meiosis
Long
Short
Division of Chromosomes.
Division of Spindle Attachments.

FIG. 90.—Diagram to show the difference inferred between two genetic abnormalities of division : (i) increased rate of contraction (shown by a wavy line) in all prophases in *Phragmatobia* ; (ii) decreased time of contraction in the prophase of meiosis in *Matthiola*. The arrow indicates the duration of contraction (from beginning of prophase to metaphase) in relation to the two fixed points, division of the chromosomes and division of the spindle attachments which comes after metaphase in meiosis (*cf.* Fig. 79).

The following examples have been found :—

1. In *Ochna serrulata*, which is optionally parthenogenetic and aposporous, unreduced nuclei in the embryo-sac mother-cell

anticipate normal mitosis by five days. The egg-cells then develop parthenogenetically (Chiarugi and Francini, 1930; *cf.* Ch. XV).

2. In *Eu-hieracium* species which are parthenogenetic, meiosis in the pollen mother-cells sets in earlier than in the sexual species (Rosenberg, 1927).

3. In a variety of *Nicotiana Tabacum* that gave unreduced gametes, variation occurred in the stage of division within single loculi of the anthers (Rybin, 1927).

4. In *Aucuba japonica* cells with restitution nuclei are relatively retarded (Meurman, 1929 *a*).

5. In *Prunus* hybrids, cells with restitution nuclei are either retarded or advanced relative to the rest (D., 1930 *a*).

6. In *Triticum vulgare*, varieties and hybrids, univalents are more frequent in retarded cells (Hollingshead, 1932).

In other new or unbalanced forms such irregularities are found without leading to failure of pachytene association, *i.e.*, without going beyond the critical point (Capinpin, 1930, on *Œnothera Lamarckiana*).

(iii) **Failure through Precocity of particular Chromosomes.** The dissimilar sex chromosomes in the heterozygous sex have the property in many organisms of passing through the stages of prophase in meiosis in advance of the autosomes (*cf.* Ch. XIV). In order to understand the cause of this behaviour it is necessary to consider all cases of the kind together. These show that the property, as it is found in the sex chromosomes, is determined genetically and not by these chromosomes being structurally dissimilar, as a superficial study would suggest. Genetically determined precocity is found in three degrees of development.

(*a*) The distal parts of all the chromosomes are precocious in *Mecostethus* (Janssens, 1924; McClung, 1928 *b*), and this is probably responsible for the localisation of pachytene pairing and chiasma formation here, in *Fritillaria*, and elsewhere.

(*b*) The whole of the sex chromosomes in the heterozygous sex where they do not pair at pachytene, whether there is a single X as in some Orthoptera and Nematoda, or both an X and a Y as in the Hemiptera. In the Hemiptera certain fragment chromosomes also show the property. These are presumably derived from the sex chromosomes, since they pair with the *Y* in *Metapodius* (Wilson, 1909), and with the *X* in *Alydus* (Reuter, 1930).

(*c*) Half the chromosome complement in certain species with an anomalous type of meiosis (*e.g.*, in *Lecanium, Pseudococcus* and *Gossyparia, v. infra*).

The property may show itself long before meiosis in the failure of the affected chromosomes to enter into a complete resting stage between divisions. In the male of the coccid *Gossyparia spuria* half the autosomes already show differential condensation in the late blastula stage (Schrader, 1929). In some groups the unpaired *X* chromosome shows progressively increased condensation during the resting stages in the spermatogonia as meiosis approaches, and consequently preserves at prophase the spiral form of the chromosome thread from the preceding division (*Tryxalis*, Brunelli, 1910, 1911; *Rhabditis*, Boveri, 1911; *Perla*, Junker, 1923; *Mecostethus*, Janssens, 1924; *Tettigonia*, Winiwarter, 1931). Generally, however, the differential condensation does not show itself before the prophase of meiosis, and is only seen in the more rapid condensation of the affected chromosomes after zygotene. From this is derived the name "chromatin-nucleoli" by which they were early described. The precocious chromosomes do not contract further than the rest at metaphase, but during the ensuing interphase they continue to show exceptional condensation. The general character of this behaviour makes it clear that we are dealing with a reaction of particular chromosomes to special genetic conditions rather than with the reaction of dissimilar homologues with one another in pairing, such as is characteristic of structural hybrids. Further critical evidence is afforded by the following observations.

(*a*) The two *X* chromosomes in the hermaphrodite generation of *Rhabditis nigrovenosa* condense precociously in oögenesis. In spermatogenesis in the same individual this precocity is perhaps exaggerated, since they fail to pair. (They divide at the first division and, lagging at the second division, they pass at random to the poles. Those with both *X* chromosomes degenerate, so that sperm are formed of two functional kinds, with and without the sex chromosome (Boveri, 1911).)

(*b*) The compound unpaired *X* chromosome of male *Perla marginata* (Neuroptera) behaves differentially in spermatogenesis, but not differentially in meiosis in an ovary-like organ produced by the male (Junker, 1923).

(*c*) Trisomic supernumerary fragments in *Fritillaria imperialis*, one of which must often be entirely unpaired, show no evidence of precocity (D., 1930 *c*), while supernumeraries in *Metapodius*, which may be present to the number of six and must be of common origin and homologous (Wilson, 1909), show strongly differential condensation.

(*d*) Precocious condensation is not usual in sex chromosomes in the homozygous sex, *e.g.*, in male Lepidoptera or female Orthoptera (Mohr, 1915), but it has been found in male *Natrix* (Reptilia) and female *Nyctereutes* (Mammalia) which are homozygous (Minouchi, 1929). It does not occur in *Enchenopa* (Homoptera), *Lebistes* (Pisces), or in angiosperms where the dissimilar sex chromosomes pair and cross over (Winge, 1923, 1930 *et al.*).

It is evident in *Mecostethus*, *Rhabditis* and *Alydus* that the precocity of identical chromosomes prevents their pairing. That this should be so follows on the precocity theory, for the earlier development of the chromosomes will compensate for the earlier prophase and restore mitotic conditions. This has been shown in *Alydus* and *Mecostethus* where the chromosomes which do not pair are already divided at the time the other undivided chromosomes are pairing. Thus precocity of the chromosomes determines their failure of pairing, not the reverse. The importance of this failure of pairing in the evolution of sex chromosomes and the development of dissimilarities between them will be considered later.

It is possible that other conditions—amongst them unlikeness of the chromosomes—may lead to a kind of precocity in development. Thus the smallest chromosome pair in *Stenobothrus* (Fig. 21) is often in advance of the rest in contraction. Differential condensation of parts of autosomes and sex chromosomes is found by Heitz (1929) in *Pellia*, though without very clear evidence of constancy (*cf.* Kuhn, 1929; Grégoire, 1932). It is found in diploid and tetraploid species of *Rosa* which are known to be hybrid (Erlanson, 1929). It is also found in possibly dissimilar pairs of chromosomes in *Brachystola* and *Arphia* (Carothers, 1913; *cf.* McClung, 1927). In one animal (*Camnula*, Orthoptera) a fragment was found to be differential when single, but normal when a second was present in the same organism through irregular mitosis (Carrol, 1920). These differences probably do depend on the relationships of the chromosomes in pairing or on their sizes, for reasons discussed earlier (Ch. X, 5).

(iv) Failure through Lack of Chiasmata. Where pachytene pairing and the meiotic contraction of the chromosomes occur normally, yet pairing fails at metaphase, this is to be ascribed to failure of chiasma formation on the analogy of the critical cases described earlier (Chs. IV and V). This has been shown directly in the first two of the following examples. A second possibility in the third case is that the chromosomes form chiasmata but fail to retain them, when terminalised, through lack of terminal affinity, but this has not yet been demonstrated.

1. The hybrid of *Lolium perenne* ($n = 7$) with *Festuca pratensis* ($n = 7$) has a slightly lower frequency of chiasmata at first metaphase than either of its parents, although pairing is perfect. Back-crosses with the *Lolium* parent fall into two sharply differing classes in regard to chiasma and pairing frequency; this must be ascribed to genetic segregation in the hybrid in factors controlling chiasma formation. The following records show the chiasma frequencies per bivalent from six complete nuclei of each plant (Peto, 1932):—

Lolium perenne, 1·81.
Festuca pratensis, 1·88.
L. perenne × *F. pratensis* (F_1), 1·71.
F_1 × *L. perenne*$_1$ { 5 plants: 1·57, 1·66, 1·66, 1·66, 1·80.
{ 2 plants: 0·80, 0·62 (defective pairing).

2. Similarly the progeny of a tetraploid ($4x = 28$) back-cross of a *Festuca-Lolium* derivative to *Festuca arundinacea* vary in chiasma and pairing frequency. Some have 14 pairs, others only 7 at meiosis; the latter have a reduced number of chiasmata per bivalent. This is another case of segregation in a hybrid (Peto, 1932).

3. A recessive "asynaptic" factor in *Zea Mays* determines

failure of pairing which is subject to rather irregular variation. Usually 0 to 2 bivalents appear, but occasionally complete pairing has been found. This resembles the variation found in certain hybrids, which are unusually susceptible to the effects of environmental conditions (*e.g., Ribes Gordonianum, v.* (Ch. VI). It is probable that the property of asynapsis is here due to failure of chiasma formation, rather than to failure of pachytene pairing from lack of precocity, since the normal meiotic contraction of the chromosomes is found. They are irregularly scattered at the first division and divide at the second. Sometimes diploid restitution nuclei are formed (*v. infra*). About half the progeny, crossed with normal pollen, are triploid ; evidently, therefore, behaviour in the embryo-sac is similar (Beadle and McClintock, 1928 ; Beadle, 1930).

Occasional failure of pairing is found both in inbred diploids (Randolph, 1928) and in an unbalanced form of maize (McClintock, 1929 *a*). Genetic conditions, less simply defined, are doubtless responsible for these abnormalities also.

4. *Crepis capillaris.* The "*X*" strain shows the hereditary property of imperfect pairing, as the following table shows.

TABLE 52

Chromosome Pairing in Two Strains of *Crepis capillaris* **and in Their Hybrids by** *C. tectorum* (Hollingshead, 1930 *b, cf.* Tables 23 and 26).

	3^{II}	2^{II}	1^{II}	0^{II}
C. capillaris (2*n*=6). Normal strain .	219	5	—	—
X strain (different plants) .	63	9	—	—
	84	62	4	—
	20	78	—	—
C. capillaris × *C. tectorum* (2*n* = 7).				
Normal strain (different plants)	47	16	—	—
	34	49	15	3
X strain (different plants) .	32	44	44	45
	16	39	31	38
C. capillaris × *C. tectorum* (3*x* = 10, C C T), believed *X* strain derivative. (*N.B.*—Trivalents rare).	usual	rare	—	—
	7^{II}	6^{II}	5^{II}	4^{II}
(4*x* = 14, C C T T, *X* strain derivative)	22	18	8	1

The character is equally pronounced in the interspecific hybrids. It would appear, therefore, that it is determined by a dominant factor or factors.

5. *Viola Orphanidis*. A similar strain with partial or complete failure of pairing has been found. The property is associated with male-sterility (J. Clausen, 1930).

6. *Triticum vulgare* (6*x*) × *T. durum* (4*x*). Certain pure lines (6*x*) selected from this cross had failure of pairing, and in some of these as many as 7 per cent. of diploid pollen grains were formed (A. A. Sapehin, 1928; L. A. Sapehin, 1931).

7. *Avena sativa* (6*x* – 2). Homozygous fatuoid segregates (Huskins, 1927; Nishiyama, 1931; 0–10^{II}).

8. *Nicotiana alata* (Avery, 1929 (2*x* + 1)).

9. *Nicotiana Tabacum* (R. E. Clausen, 1930, 1931 (4*x* – 1)).

10. *Primula kewensis* (Newton and Pellew, 1929 (4*x* – 2)). These forms are unbalanced and have incomplete pairing, evidently genetically controlled, since the same chromosomes pair in the balanced forms.

11. *Pygæra pigra* ($n = 23$) × *P. curtula* ($n = 29$) (Federley, 1930). The progeny of this cross have 52 chromosomes, but whereas the female has as many as 23 pairs the male has little or no pairing. This difference is evidently decided by a genetic sex-linked or sex-limited character. The result is of interest, for while the female gives eggs with the reduced chromosome number, the male by double division of the univalents (*v. infra*) gives diploid unreduced sperm which yield triploids on back-crossing. In these another difference is found between male and female, for although one haploid set is left unpaired in both, in the male these univalents divide twice (again giving diploid sperm), and in the female the univalents are lost (again giving haploid eggs). Back-crossing of the male, therefore, continually yields triploids.

12. *Smerinthus populi* × *S. p.* var. *astauti* (Federley, 1915). In this hybrid, similarly, the female has more pairing than the male, often complete pairing (27 to 28 pairs instead of 23 to 28 pairs (*cf.* also Chiarugi, 1926, on *Artemisia nitida*, and *Drosophila*, p. 284).

13. A triangle of crosses in *Viola* (J. Clausen, 1931 *c*) reveals a genetic difference governing the frequency of pairing.

Viola nana (24) × *V. tricolor* (13)	16–18^{II}
V. tricolor × *V. arvensis* (17)	13^{II}
V. nana × *V. arvensis*	2^{II}–6^{II}

Since pairing not only takes place completely between the *tricolor* chromosomes and those of *nana*, but also by autosyndesis within *nana* in the hybrid, and pairing is also complete between *tricolor* and *arvensis*, it might be expected that a considerable amount of pairing would occur in the third hybrid of the triangle. Its almost complete failure is therefore a strong indication that the genotype of this hybrid determines the reduction of pairing.

14. *Digitalis lutea* ($n = 56$) crossed by *D. purpurea* ($n = 28$) and *D. lanata* ($n = 28$) gives hybrids with no pairing (Haase-Bessel, 1922), while *D. lutea* crossed by the closely related species *D. micrantha* ($n = 28$) gives complete pairing, including autosyndesis. This shows that different genetical conditions determine different behaviour of the homologous chromosomes within the haploid complement of *D. lutea* (either in chiasma formation or precocity).

15. *Chrysanthemum.* In crosses of the decaploid *C. marginatum* with different species, its chromosomes show a different degree of pairing with one another. One cross has complete autosyndesis, the other probably complete absence of it. This is to be attributed to different genetic conditions determining chiasma formation in the two hybrids (Tables 28 A and B).

16. *Ægilops triuncialis* ($n = 14$) × *Secale cereale* ($n = 7$). Five to seven pairs are formed, evidently by autosyndesis of *Ægilops* chromosomes; less pairing occurs in hybrids with more closely related species. Evidently genetic conditions control this difference, since the same pairs of chromosomes are concerned (*v.* Berg, 1931, *a* and *b*; *cf.* Kihara, 1931, Table 23).

17. Kihara (1929) finds that various *Ægilops-Triticum* hybrids have bivalents and trivalents. The trivalents show the occurrence of autosyndesis and allosyndesis together, while bivalents show one or the other. From their frequency, the relative frequency of these two kinds of pairing can therefore be calculated. They show a positive correlation which indicates the effect of genetical and environmental factors on pairing.

It may be argued that, if in these cases reduction or failure of pairing of the chromosomes at meiosis may be determined by a genetic property, such may equally be the explanation of a failure in first-generation hybrids. In fact, genetic conditions do influence the failure to a certain extent in particular instances (as pointed out in *Chrysanthemum* and *Digitalis* crosses), but that a genetic property is not the essential factor may be shown in two ways :—

(i) Failure of pairing in hybrids is to be predicted from the observation that structural differences distinguish species and that structural hybridity even in its simplest form (from single changes) reduces pairing—and crossing-over.

(ii) When the diploid hybrid yields a tetraploid by doubling, each chromosome having an identical mate, pairing is completely restored, as would be predicted on the assumption that it is the differences of structure which hinder pairing, but not on the assumption that the failure is a genetic property. Doubling of the chromosome number in one of the forms just described, on the other hand, does not restore complete pairing (*v.* Table 52).

(v) **Exceptional Failure in Normal Forms.** Three causes of failure of pairing have been identified, *viz.*, structural or numerical hybridity, genetic-environmental reaction, fragmentation. Apart from any such exceptional conditions it happens that two homologous chromosomes occasionally fail to pair, in the following species :—

TABLE 53

Exceptional Failure of Pairing

Diploids	
Nicotiana alata ($2n = 18$)	Ruttle, 1927 ; Goodspeed and Avery, 1929 *a*.
Zea Mays ($2n = 20$)	Randolph, 1928.
Ranunculus acris ($2n = 14$)	Sorokin, 1927 *b* ; Larter, 1932.
Cycas revoluta ($2n = 22$)	Nakamura, 1929.
Dorstenia plumariæfolia ($2n = 26$).	Krause, 1931 (? fragments).
Crepis capillaris ($2n = 6$)	Hollingshead, 1930 *b* (*v. supra*).
Scilla italica ($2n = 16$)	Dark, 1932 *c* (Fig. 91).
Trimerotropis citrina ♂ ($2n=23$)	Carothers, 1931.

(unequal bivalent, perhaps owing to deficiency, fails to pair 8 times in 52 divisions).

Triploid	
Narcissus poetarum ($3x = 21$)	Nagao, 1929 ($6^{\text{III}} + 3^{\text{I}}$).
Tetraploids	
Nicotiana Tabacum ($4x = 48$)	R. E. Clausen, 1930, 1931.
Prunus Cerasus ($4x = 32$)	D., 1928.
Primula sinensis ($4x = 48$)	D., 1931 *a*.
Campanula persicifolia ($4x = 32$).	Gairdner and D., 1931.
Triticum durum ($4x = 28$)	Thompson and Robertson, 1931.
Tulipa stellata ($4x = 48$)	D. and Janaki-Ammal, 1932.
Kniphofia sp. ($4x = 24$)	Moffett, 1932.
Hexaploids	
Triticum vulgare, etc. ($6x = 42$)	Thompson and Robertson, 1931 ; Hollingshead, 1932.
Octoploid	
Bromus erectus, eu-erectus ($8x = 56$).	Kattermann, 1931 (*v*. Table 30).

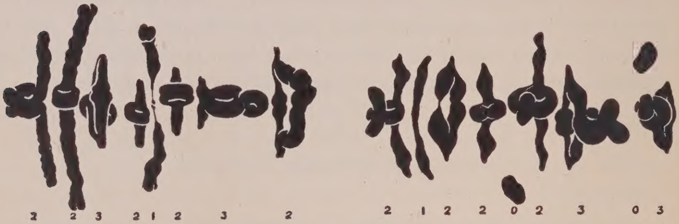


FIG. 91.—Side views of two first metaphases in *Scilla italica* ($n = 8$), the chromosomes drawn separately. The numbers of chiasmata are given below each bivalent. Right : the two shortest chromosomes are unpaired, having failed to form one chiasma. An example of lack of adaptation of chiasma frequency to the range of chromosome size as in organisms with new fragments. (Reproduced by kind permission of Mr. S. O. S. Dark.)

In the diploids it is noticeable that the chromosomes affected are usually the shortest. This failure to pair may therefore be looked upon as the direct result of random failure to form a chiasma. In *Crepis* the failure was found in the diploid tissue of a haploid, and abnormal developmental conditions are therefore responsible.

With the same average chiasma frequency all bivalents would occasionally fail to pair in the absence of interference (Ch. X).

In polyploids different conditions are responsible. In autopolyploids exchanges of partner will often prevent pairing from being complete (as shown earlier in the long chromosomes of *Hyacinthus*, Ch. IV). In allopolyploids it is also possible that beyond a certain point increase in the number of chromosomes will lead to difficulty in their finding their partners at zygotene.

2. IRREGULARITIES OF MEIOSIS

(i) **Classification.** Irregularities are important in relation to both their causes and effects. They may accordingly be classified as follows :—

TABLE 54

Conditions of Abnormality in Meiosis

Proximate Cause.	Remote Cause.	Effect.	Occurrence.
A. Failure of chromosome pairing (from (i) and (ii)).	(i) Hybridity (sensu stricto)	Production of too many or too few nuclei.	(i) Hybrids.
	(ii) Genetic property.		(ii), (iii) Mutants, or segregates of hybrids.
B. Failure of spindle mechanism (from (ii) and (iii)).	(iii) External or developmental conditions.		
A. and B. combined (from (iv)).	(iv) Genetic adaptation. (*a*) following hybridity. (*b*) without hybridity.	Regular formation of two diploid nuclei.	(iv) (*a*) Diploid parthenogenesis. (iv) (*b*) All facultative and cyclic parthenogenesis. (Ch. XIV).

(ii) **Irregularities Due to Failure of Pairing.** The best example of a hybrid with complete failure of pairing leading to a variety of aberrant results is *Raphanus-Brassica* (Karpechenko, 1927 *a*). There is no essential distinction between its behaviour and that of a haploid (*v. infra*). Eighteen univalent chromosomes are scattered over the spindle at a stage that would normally be metaphase. Some of these come on to the equator and divide before the spindle disappears, but frequently a single nucleus is re-formed, containing the eighteen undivided chromosomes. This is known as a restitution nucleus (Rosenberg, 1927). Occasionally a few chromosomes may be left out to form a second smaller nucleus which has a separate second division.

Whether one or more nuclei are formed around the scattered chromosomes after the first division, they divide at the second with the division of all those chromosomes that have not already divided; those that have already divided lag, so that they may be lost in the cytoplasm. A common result is therefore the formation of two nuclei (a dyad) each having the numerically and genetically unreduced number of chromosomes. It also happens in other

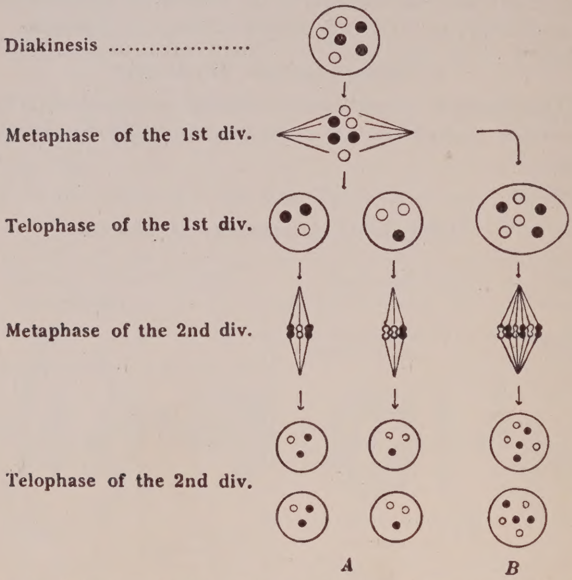

Diakinesis
Metaphase of the 1st div.
Telophase of the 1st div.
Metaphase of the 2nd div.
Telophase of the 2nd div.
A
B

FIG. 92.—Diagram showing two types of meiosis undergone by pollen mother-cells in *Raphanus-Brassica* and other hybrids, *A* giving irregularly reduced and functionless gametes, *B*, unreduced and fertile gametes following formation of a restitution nucleus. (From Karpechenko, 1927 *a*. *Cf.* Fig. 105.)

hybrids (*e.g.*, *Prunus*), and probably in this one, that the second division may fail as well as the first and give rise to a single tetraploid nucleus.

Sometimes counting of the chromosomes at the second division shows that the univalents which have divided at the first division divide again at the second, but this only happens regularly in the *Pygæra* and other lepidopteran hybrids. Following almost complete failure of pairing the univalents divide at both divisions, which in consequence take a very regular course and regularly give diploid gametes (Federley, 1913, 1914, 1930 ; Cretschmar, 1928).

In the following instances double division of univalents has been seen or inferred :—

Pygæra hybrids . . .	Federley, *l.c.*
Rosa canina . . .	Täckholm, 1922.
Rosa subglauca . . .	Erlanson, 1929.
Raphanus-Brassica . .	Karpechenko, 1927, *a* and *b*.
Prunus avium nana . .	D., 1930 *a*.
Saccharum officinarum . .	Bremer, 1929.
Ribes hybrids . . .	Meurman, 1928.
Brassica, hybrids . .	Morinaga, 1929.

When several of these abnormalities of meiosis are combined and syndiploidy also occurs in the spore-forming tissue (Ch. III) tetraploid and octoploid gametes may be formed (*e.g.*, in *Prunus*), and the first have been shown to function by an examination of the progeny in *Raphanus-Brassica*.

The irregularity which results from failure of pairing due to genetic causes (A. (ii)) is indistinguishable from that occurring in haploids and hybrids.

(iii) Irregularities due to Failure of the Spindle Mechanism. Where there is failure of pairing at meiosis the mechanism of suppression is not usually competent to give a regular result. But in a number of plants it has been possible by treatment with reagents or abnormal temperatures (B (iii)) to suppress the first division, although the chromosome pairing is unaffected. Evidently, therefore, the mechanism of separation, which we may call the spindle mechanism, may be independently considered (*cf.* Ch. XII).

Recently a few cases of genetic conditions producing a similar change have arisen (B (ii)). This leads either to the formation of numerous small nuclei (in *Triticum*) or the failure of a wall to form between two daughter-nuclei, a process shown by Belar and others to be intimately connected with the spindle, so that they later often fuse.

In *Kniphofia Nelsonii* (Moffett, 1932 *a*), a series of abnormalities occur during or after meiosis, apparently according to the time at which spindle degeneration sets in. This probably varies with the position of the flowers in the spike. In the extreme case the chromosomes form, instead of two nuclei at the end of the first division, a number of scattered nuclei which develop separately. If the first division proceeds regularly the same abnormality may befall the second division, and where this also is regular a wall may fail to form between two or all four of the daughter-nuclei. In consequence, these, or the numerous irregular nuclei, often fuse during the first mitosis of the single or double giant pollen grain. Side by side with these abnormalities normal tetrads are formed. The normality is apparently genetic and the gradation in its expression depends on differences in developmental conditions. This is particularly clear because in *Zea Mays* an analogous property is determined by a recessive factor (Beadle, 1932).

In *Hyacinthus*, Stow (1930) has induced repeated division of the generative nucleus in the pollen grain in such a way as to give it the character of an embryo sac, having eight or more nuclei. In maize a second genetic factor produces a result which combines in effect the abnormalities of *Hyacinthus* and *Kniphofia* (*v. infra*). These instances show still more clearly the genetic control of the spindle and its independence in cause of chromosome pairing.

What may be regarded as the extreme examples of failure of the spindle are found in the parthenogenetic plant species, *e.g.*, *Euhieracium* (Rosenberg, 1917, 1927). In these the chromosomes never emerge from the nucleus for the first division, but at a stage corresponding to diakinesis the nucleus contracts, reverts partially to a resting stage, and then carries out a single division corresponding to the second division. All the stages in the development of this process (which gives regular failure of reduction) are known in

Hieracium, from that in which simple lack of pairing leads to the formation of restitution nuclei. It therefore seems as though this perfected mechanism had arisen in hybrids as an adaptation by selection for the genetic property of spindle suppression (Chs. XV and XVI).

Genetic control of the spindle and of its relation with particular chromosomes has played an important part in the evolution of parthenogenetic as well as sexual systems. It may be inferred *inter alia* from the following examples :—

(i) Sex chromosomes at anaphase where they are unpaired do not follow the haphazard methods of *new* unpaired chromosomes in hybrids, but as a rule regularly follow or precede the autosomes.

(ii) The spindle has been modified in its relation to the chromosomes at the first division in haploid Hymenoptera so as to lead to no separation of daughter chromosomes.

(iii) One X chromosome is allowed to lag and be lost at the single meiotic division in Aphides whose eggs are to yield males. Thus the parthenogenetic female with $2A + 2X$ chromosomes gives progeny with $2A + X$ chromosomes (Morgan, 1915).

(iv) In *Angiostomum* (Boveri, 1911; Schleip, 1911) the hermaphrodite condition arises in parasitic individuals of the same chromosome constitution as that of non-parasitic females (*i.e.*, two sets of autosomes and two X chromosomes—$2A + 2X$). These produce a proportion of sperm lacking one X chromosome owing to failure of pairing of the X's and the lagging at the second division (*v. supra*). Hence a proportion of the progeny are males with $2A + X$ chromosomes. Only the $A + X$ sperm of these is functional, hence an alteration of sexual and hermaphrodite generations. It is unnecessary to suppose (*cf.* Witschi, 1929) that because genetic control determines loss of an X in Aphides and *Angiostomum* the X does not itself directly control sex.

(v) Meiosis in *Rosa canina*, *Coccidæ*, *Sciara*, etc. (*v. infra*).

These observations show that the mechanism of the spindle is genetically independent of chromosome behaviour, and therefore capable of adaptation. This has led to the co-ordination which secures regular reduction in normal meiosis as well as to the special adaptations referred to above and discussed in Chapter XV.

TABLE 55

Cases of Suppression of First of Second Division
(*cf.* Table 54).

A. (i) Failure of Pairing; due to hybridity (*v.* also Haploids and Parthenogenesis).

α. General Hybrids.

Drosera (3*x*)	Rosenberg, 1909.
Papaver	Yasui, 1921; Ljungdahl, 1922.
Saccharum	Bremer, 1923.
Triticum-Secale	Kihara, 1924.
Syringa	Florin, 1926.
Nicotiana (3*x*, 5*x*, etc.)	Goodspeed, 1927; Rybin, 1927; Brieger, 1928.
Petunia	Matsuda, 1927.
Prunus (2*x*, 3*x*, 6*x*)	Kobel, 1927; D., 1930 *a*.
Œnothera (4*x*)	Schwemmle, 1928.
Ribes	Tischler, 1928.
Digitalis	Buxton and Newton, 1928.
Canna aureo-vittata gigas	Honing, 1928.
Triticum-Ægilops	Kagawa, 1929; Kihara, 1931; Kihara and Katayama, 1931.
Aucuba japonica	Meurman, 1929 *a*.
Triticum hybrid (3*x*)	Thompson, 1931.

β. Purely Numerical Hybrids.

Datura (3*x*)	Belling and Blakeslee, 1922.
Solanum (3*x*)	Jørgensen, 1928.
Tulipa (3*x*)	Newton and D., 1929.
Tradescantia (3*x*)	D., 1929 *c*.
Salix (3*x*)	Håkansson, 1929.

(ii) Due to a Genetic Property (*cf.* Section 4).

Perla marginata (♂)	Junker, 1923.
Avena sativa ($6x - 2$)	Huskins, 1928; Nishiyama, 1931.
Nicotiana alata ($2x + 1$)	Avery, 1929.
Zea Mays (asynaptic)	Beadle, 1930.

All cases of facultative and cyclic parthenogenesis with suppression of the first division (*v.* Ch. XV).

B. (ii) Failure of Spindle ; due to genetic property.

Triticum vulgare var.	L. A. Sapehin, 1931 (probably several recessive factors).
Kniphofia	Moffett, 1932.
Hyacinthus orientalis	De Mol, 1924 ; Stow, 1930.
Zea Mays	Beadle, 1932.

A. and B. (iii) Due to External Conditions (effect shown by abnormal treatment).

Vicia	Sakamura, 1920.
Funaria	v. Wettstein, 1924.
Epilobium	Michaelis, 1926.
Gagea	Sakamura and Stow, 1926.
Liriope, Scilla	Shimotomai, 1927.
Lychnis	Takagi, 1928.
Triticum	Bleier, 1930.

(iv) **Meiosis in Haploids.** Meiosis from diakinesis to tetrad formation has been described in the following true haploids (*cf.* Ch. XV for meiosis in male animals).

Datura Stramonium	Belling and Blakeslee (1923, 1927).
Matthiola incana	Lesley and Frost, 1928.
Nicotiana glutinosa	Goodspeed and Avery, 1929.
Nicotiana Langsdorffii	Kostoff, 1929.
Crepis capillaris	Hollingshead, 1930 *a*.
Œnothera franciscana	Emerson, 1929. Davis and Kulkarni, 1930. Stomps, 1930, *a* and *b*.
Œnothera rubricalyx	Gates and Goodwin, 1930.
Œnothera blandina	Catcheside, 1932.

The following general description applies to all these forms. The chromosomes show no association at diakinesis ; the haploid number of univalent chromosomes is distributed evenly in the nucleus. (Exceptions to this rule have been considered earlier, *v.* Ch. IX.) At a stage corresponding to metaphase the spindle is formed and the chromosomes may either be distributed at random over it or, less commonly, form a metaphase plate. In the former case the chromosomes will be distributed at random to the two poles, as usually observed. In the latter case they will divide, their halves passing equally to the two poles. Where, however, a few come on to the equator, these divide; the rest remaining scattered on the spindle are carried by its expansion towards the poles (*cf.* Ch. II), and are included in daughter-nuclei if they lie close enough together.

In these ways two or more daughter-nuclei are formed, according to whether the chromosomes are collected or scattered. If they are not even separated into two groups a single nucleus—a "restitution nucleus"—is formed embracing all the chromosomes. It is probable in *Matthiola* that this formation of a restitution nucleus supervenes before the spindle is completely organised. The observation of divided univalents at diakinesis in haploid *Crepis* is perhaps due to the same suppression of the first division. The diakinesis was really interphase in a restitution nucleus. Such a nucleus undergoes a single division that really corresponds to the second division, to give "dyads" of which an extremely high proportion are formed.

Where two nuclei are formed they may undergo a second division, at which there divide the chromosomes which have not already divided. Where most of them have already divided this division may be suppressed to give a single daughter-nucleus. In *Œnothera*, Davis and Kulkarni consider that a unipolar spindle is often formed at the first division so that the chromosomes pass to one pole and a single (diploid) nucleus is reconstituted, but it is doubtful whether such a novel mechanism can be inferred.

Thus meiosis may yield one, two, three, four or a larger number of daughter cells. In *Datura* the proportions of the different results are very variable, 5 and 17 per cent. of the pollen grains were found as dyads in different estimations.

From the suppression of either the first or the second division unreduced gametes are formed. These are haploid—or approximately haploid, for the irregularity of division does not permit of a regular result and an undivided, double, chromosome may be included in one of the daughter-nuclei. In this way haploid plants often give diploid or trisomic seedlings, at least when the pollen of diploids is used on them. In *Datura* 12 per cent. of non-abortive pollen grains are produced. These are the same size as the pollen grains of diploids and must contain the full haploid complement. 393 selfed seedlings of a haploid *Datura* were all diploid, apart from twelve trisomic plants ($2x + 1$). Stomps found both triploid and trisomic plants in the progeny of haploids.

It is particularly clear in the *Triticum* and *Nicotiana* " haploids " (*v.* Ch. VI) that irregularities were localised, that is to say, in one anther regular tetrads were largely produced, in another irregular ones. This is characteristic of most irregularities following failure of pairing at meiosis, for while the formation of the spindle is clearly co-ordinated with that of bivalents, it is not so co-ordinated with that of univalents in new hybrids and haploids. Local differences account for the wide variation in the proportion of good pollen in *Datura*.

Finally, syndiploidy, or the fusion of two pollen mother-cells, with probable fusion of their nuclei, has been found in haploid *Crepis*, and in *Triticum*, where fusion occurred between whole groups of pollen mother-cells.

TABLE 56

Arrangement of Cells in " Tetrads " of Haploid Plants

	Monads.	Dyads.	Triads.	Tetrads.	Pentads.	Hexads.
Datura (1867) .	—	187	(a few)	1385	73	205
Matthiola (406) .	3	285	99	19	—	—
Crepis (282) . .	12	195	57	19	—	—

Following the type of meiosis observed, it is to be expected that haploid plants will be very infertile and that all their viable progeny will be diploid or approximately diploid. This is the case, as the following results show :—

Datura (Blakeslee and Belling, 1927). Selfed : 381 probable diploids, 12 trisomics.

Solanum Lycopersicum (Lindstrom, 1928). No selfed seed. 42 seedlings from 100 fruits with pollen of diploid.

Nicotiana glutinosa (Goodspeed and Avery, 1929). No seed when selfed or crossed reciprocally with diploid.

Nicotiana Langsdorffii (Kostoff, 1929).—No selfed seed, few seeds when crossed with pollen of diploid.

Nicotiana Tabacum (Clausen and Mann). No seeds.

Œnothera franciscana (Davis and Kulkarni, 1929). Selfed : 694 diploid, 29 haploid, 17 mutant diploid.

Crossed on diploid : 297 diploid.

Crossed by diploid : 234 diploid, 2 mutant diploid.

(v) **Conclusions.** The behaviour of the chromosomes at meiosis in haploid plants is conditioned by their failure of pairing. It follows the same course of irregularity and has the same results (formation of unreduced gametes, and so on) as in hybrids and genetically abnormal plants with largely or entirely unpaired chromosomes. The variation in this behaviour may be supposed to be conditioned by differences in the time-lag of the division of the spindle attachments of the chromosomes after the formation of the spindle. Where the division takes place too long after the formation of the spindle the unpaired chromosomes fail to orientate themselves on the equator and many nuclei are formed. In an intermediate condition some of the chromosomes arrange themselves on the equator and begin to divide before the spindle disappears. A single nucleus may then be formed. Finally, where the division of the attachments follows quickly, most of the chromosomes divide regularly at the first division ; two nuclei are formed and the daughter chromosomes either lie without division on the second division plate and single nuclei are reconstituted, or they divide a second time. In either case they give diploid nuclei. The variation in degree of synchronisation is to some extent specific. In pollen mother-cells of *Rosa* univalents divide regularly at the first division, in *Hieracium* rarely. Hence arises the difference in results of meiosis in different haploids and hybrids.

3. THE IMITATION OF MEIOSIS : POLYMITOSIS

Meiosis may be more or less effectively replaced by mitosis under special genetic conditions—less effectively in adventitious mutants such as asynaptic maize, more effectively in races with adaptive parthenogenesis (*v.* Ch. XV). It is equally to be supposed that mitosis might under special genetic conditions be replaced by meiosis.

This is possibly so at an early stage in the testis of *Icerya* and in the antheridia in the diploid gametophytes of some aposporous ferns (*v*. Chs. XV and XVI) where the normal occurrence of meiosis is also omitted, in compensation. The simple intercalation of meiosis is, of course, bound to be destructive of the normal sexual cycle, and cannot therefore be expected save as an adventitious mutation. In this way it seems to have been discovered in the form of supernumerary divisions in the pollen grains of races of *Zea Mays* by Beadle (1931). This property of having " polymitosis " is inherited as a mendelian recessive character.

In an abnormal plant the four nuclei of the pollen tetrad formed by a normal meiosis enter into a prophase condition soon after the end of the second division. The chromosomes are still single at the early stages but are certainly sometimes double at metaphase, when it is found that occasional pairs are formed with interstitial and terminal chiasmata (Plate VII). At metaphase the chromosomes have the extra contraction found at meiosis ; they sometimes form a metaphase plate, but they are usually scattered over the spindle and are distributed at random to the two poles at anaphase. The chromosomes have not been seen to divide, but probably do so occasionally. This division is followed immediately by two more, and cell-walls are formed between the products. Thus 40 chromosomes or a few more are distributed to 32 cells, most of which presumably have only one chromosome. Fragments are occasionally found. The pollen is entirely sterile, but nearly 10 per cent. of the embryo-sacs are viable and haploid, probably owing to the failure to form separate daughter-nuclei after division.

It will be observed that the first of these divisions has the property of beginning precociously, which in itself enables one to predict its later course on the precocity theory. This division corresponds in all essentials to the first meiotic division in a haploid. The occurrence of pairing is analogous to that at meiosis in haploid *Œnothera* (*v*. Ch. IX). The appearance of fragments is expected on the chiasmatype hypothesis because crossing-over at chiasmata between relatively translocated segments will give new chromosome types large and small.

The abnormality differs from meiosis in that it is *reiterative ;* the conditions that determine it persist as long as there are chromosomes to divide, while in meiosis it is assumed that the special conditions determining precocity act once for all at the prophase of the first division and only determine the second division through their effect on chromosome behaviour at the first.

4. ABNORMAL FORMS OF MEIOSIS

(i) **Introduction.** There are a number of instances of partial or complete substitution of the ordinary mechanism of pairing and segregation of chromosomes by a new mechanism so different from the old that their relationship cannot yet be clearly traced. The potentiality for developing such anomalies is seen in the substitution of normal chiasma pairing by terminal affinity in certain chromosomes in the Hemiptera (Ch. XII) and in the genetical anomalies of the spindle referred to above. Some of these are unique in their properties, others occur in series showing the development of the system.

In either case such systems must be supposed to have developed gradually and to have been perfected adaptively, for the differences distinguishing them from the normal are numerous and co-ordinated to give a regular result. They depend both on changes in the behaviour of the chromosomes and on changes in the behaviour of the spindle mechanism. The two most interesting will be described.

(ii) **In Rosa canina.** All species of *Rosa* have multiples of 7 chromosomes. Aneuploid forms reported by Täckholm (1922) and Erlanson (1929) are exceptional and probably sterile. Most diploid and even-multiple polyploid species have fairly regular pairing, although they are none the less to be regarded as hybrids (Blackburn and Harrison, 1921; Täckholm, 1922; Erlanson, 1929), and some have been shown to be interchange heterozygotes (Erlanson, 1931 *c*). They are sexually reproducing, with occasional apomixis in some species. All species of the section *Caninæ* (European and Asiatic) are facultatively apomictic. For example, in 38 seedlings of *R. coriifolia solanifolia* × *glauca concolor*, 37 were maternal in character, one was a hybrid (Täckholm, 1922). Gustafsson (1931) has shown that this apomixis is not spontaneous, but requires the stimulus of pollination, especially of cross-pollination, and self-fertilisation probably leads to successful sexual reproduction (*cf.* Ch. XV, pseudogamy).

All the *Caninæ* roses have, according to Täckholm and Hurst (1931), seven pairs of chromosomes and 21 univalents (or, in a few species, 14 or 28). The pairs are distinguished by the regularity of their occurrence and of their form. Erlanson (1931) has shown that metaphase pairing is of the partially terminalised type in *Rosa*. Uniformity probably means therefore that while in other groups of *Rosa* the chromosomes may be united by chiasmata at one or both ends, in the *Caninæ* they are always united at both ends, and this is an indication of regularly high chiasma frequency and homozygosity as to the pairs. Pairing behaviour is identical in embryo-sac and pollen mother-cells (Fig. 93), but the mechanism of distribution is entirely different. In the pollen mother-cells the bivalents and univalents lie in one equatorial plate. The bivalents divide first and then, as is usually the case, the univalents lying between the separating groups of daughter bivalents divide and follow them to the poles with very little irregularity. At the second division the same process is repeated ; the daughter bivalents divide again and the daughter univalents also proceed to divide a second time (like the unpaired chromosomes in *Pygæra* hybrids). The delay, however, is greater than at the first division. Most of the univalents fail to reach the poles and many are left on the plate. In consequence many nuclei of irregular size are formed and the 4 nuclei which have received the 7 chromosomes derived from the bivalents have in addition a varying number of chromosomes derived from the univalents. Examination of the first mitosis in the pollen grains of *R. tomentella obtusifolia* and *R. seraphini* ($2n = 5x = 35$) showed the following chromosome numbers (*cf.* Table 38) :—

7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
9	23	13	7	4	1	1	—	1	—	1	1	—	1	—	1

These do not necessarily correspond with the numbers originally received, but they indicate the iregularity of the process and the relatively high proportion that receive the simple haploid complement.

Several embryo-sac mother-cells are found in each ovule of these roses, and they are therefore exceptionally favourable for study.

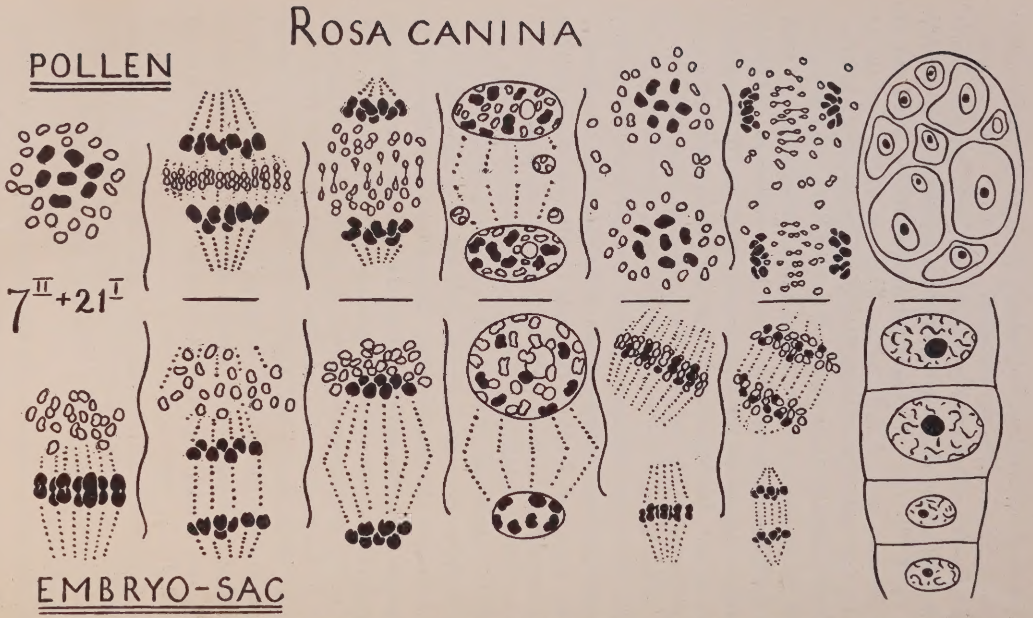

ROSA CANINA
POLLEN
$7^{\text{II}}+21^{\text{I}}$
EMBRYO-SAC

FIG. 93.—Diagram showing the different methods of division in the pollen and embryo-sac mother-cells of a pentaploid *Rosa canina*, with 7 paired and 21 unpaired chromosomes, shown black and in outline respectively (after Täckholm, 1922). The stages from left to right are: first metaphase, anaphase, late anaphase, interphase, second metaphase, second anaphase, "tetrads" (*v.* Text).

At metaphase the unpaired chromosomes, instead of lying in the same plate as the bivalents, are all, or almost all, grouped at the micropylar pole of the spindle, where they are joined at the first telophase by the seven daughter bivalents going to this pole. In the pentaploid forms there are therefore usually 28 chromosomes at the micropylar end and 7 at the chalazal end. The second division is regular and yields two small nuclei and two large ones; one of the latter gives the functional embryo-sac, as is shown by the chromosome numbers of hybrid seedlings.

Self-fertilisation of these plants will therefore yield offspring like the parent having 7 pairs of chromosomes of identical origin and 21 chromosomes that are not directly related to them or to one another. A complement of a race of such a kind consists of 7 pairs of chromosomes that are transmitted by sexual reproduction (and no doubt inbred and homozygous) together with 21 chromosomes that are transmitted virtually by vegetative processes, for they are neither separated by meiosis nor brought together by fertilisation. Reproduction, in fact, may be described as *semi-clonal*. In regard to its genetic effect this mechanism is analogous with polyploidy and with the ring formation of complex heterozygotes, inasmuch as it enables a hybrid to breed true. The mechanism is responsible for the extreme constancy of the innumerable species of Caninæ. It is also responsible for the ability of widely distinct forms to hybridise. The seven chromosomes of the pairs are probably highly constant throughout the group. Their pairing alone is necessary for fertility. The unpaired chromosomes are, on the other hand, the organs of variation. In this specialisation of function the two groups of chromosomes are analogous to the differential and the homozygous regions of the chromosomes of the heterozygous *Œnothera* species.

The origin of the system does not present much difficulty. Repeated crosses amongst diploid species or a cross between two hexaploid species would give the condition with seven pairs of chromosomes and twenty-eight univalents, as in *Triticum-Ægilops* crosses. (It is not now necessary to suppose, as Täckholm did, a cross between a diploid and an imaginary decaploid as the source of such a form.) The hybrid would give at once a proportion of pollen grains with only the seven chromosomes derived from the pairs. The essential new property of these forms is therefore the polarisation of the embryo-sac mother-cell whereby it regularly gives embryo-sacs containing the full set of unpaired chromosomes. This property and the perfection of the mechanism of division in the pollen mother-cells must have been achieved by adaptation in the course of sexual reproduction. Täckholm's objection to this is also no longer valid. He considered that it would lead to frequent aneuploid forms in nature, but we now know that such forms would be largely eliminated (*cf.* Ch. IX). Probably apomixis observed in the Caninæ roses depends on the stimulus of cross-pollination, and sexual reproduction is the rule. No cytological evidence of nucellar embryony or other apomictic processes have yet been obtained, in spite of prolonged search (Hurst, 1931). The present account, therefore, seems to provide a sufficient explanation of the origin and behaviour of the system.

(iii) **In the Coccidæ.** In the coccids *Pseudococcus* (♀, $2n = 10$) and *Protortonia* (♀, $2n = 6$) the haploid number of bivalents are formed in oögenesis and meiosis is normal (Schrader, 1923, 1931). In the male *Pseudococcus* ($2n = 10$) five of the chromosomes condense prematurely at the prophase of meiosis; they do not pair with the other five and the first division is equational. At the second division the precocious chromosomes pass to one pole and the others then pass to the opposite pole. The two sides of the spindle are formed separately, as in the haploid bee, where only one side is effective. It appears that the two sets of five chromosomes are those derived from opposite parents, and that they are therefore permanently separated in phylogeny. The whole set is differentiated in regard to sex. The behaviour in another coccid, *Lecanium hemisphericum*, is similar (Thomsen, 1927).

In the male *Protortonia* ($2n = 5$), on the other hand, the condition is probably intermediate between that in *Pseudococcus*, and in the normal type of sex-determination in other Hemiptera. There is no distinction between the two sets, and pairing takes place between two chromosomes, the other three remaining unpaired. The four groups lie in separate vesicles at the first division and the chromosomes divide equationally. But at the second division the chromosomes arrange themselves in a row or chain which lies axially in the spindle and divides so that two chromosomes at one end go to one pole and the other three to the other. Their order is not constant, but one of the chromosomes which is definitely smaller than the rest lies at one end of the chain in three-quarters of the nuclei. This is probably the arrangement giving the effective segregation, which in this case is of one kind only—probably that giving the separation of unchanged maternal and paternal chromosomes. Diagrammatically, on this hypothesis, the chromosome relationship can be represented thus: ♀, $AABBCC$; eggs, ABC; ♂, $AABB_1C$; sperm, ABC (♀-producing); and AB_1 (♂-producing). Since B and B_1 have no opportunity of crossing over, and B_1 is transmitted exclusively by the male sex, they will be permanently separated in phylogeny (as the whole complexes are in *Pseudococcus*). It may be noted parenthetically that it does not necessarily follow that they are not homologous or even identical because they fail to pair, for genetic factors must undoubtedly have been the original cause of this failure (as in facultative parthenogenesis, *q.v.*). But it does follow that since they do not pair, but yet are segregated to opposite sexes they will vary independently in so far as they vary at all and therefore become less and less like one another as evolution proceeds.

In another Coccid, *Llaveia bouvari*, a condition is found more nearly approaching normal meiosis (Hughes-Schrader, 1931). The chromosomes as a rule pair normally, even forming chiasmata apparently, though each pair remains in a separate vesicle. Occasionally, however, one pair associates at metaphase only, as in *Protortonia*.

These species are most easily considered as representing steps in the successive differentiation of the two sets of chromosomes in the male, so that the whole of a set develops the character of X or Y and the " Y " set is carried exclusively in the male line. Such a differentiation might be conditioned by, first, the replacement of ordinary chiasma-pairing by pairing as found in the sex chromosomes of other Hemiptera, which seems to depend on the property of terminal affinity, and, secondly, the development through genetic change of a special spindle mechanism. The progressive change in this series is represented in the diagram (Fig. 94). It is described here as differentiation, meaning the accumulation of structural differences. It has been described by the Schraders as "degeneration"—a term which should be avoided in speaking of chromosomes here and elsewhere, because it implies an analogy with evolutionary changes in gross structures that is somewhat misleading.

But there is a fourth genus, *Gossyparia*, whose behaviour seems to conflict with this or any other evolutionary hypothesis, although the Schraders have represented it as the last step in the process of differentiation. Here again meiosis is normal in the female: 14 bivalents are formed. In the male half the chromosomes are precocious and do not associate with the other half, but they do pair at metaphase amongst themselves. It is believed that this is not true pairing and does not lead to segregation, all 28 chromosomes dividing equationally at the first division. The precocious

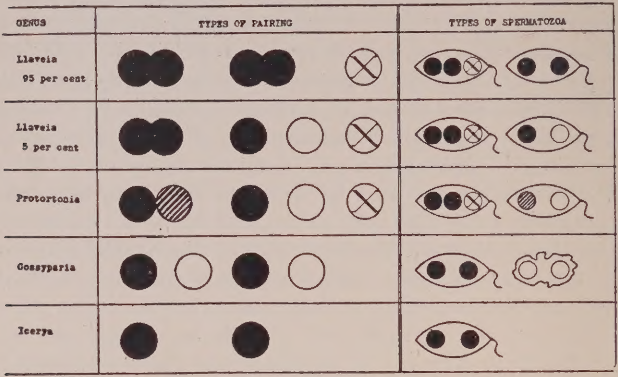


FIG. 94.—Diagram of chromosome behaviour at meiosis in the male in a series of forms showing a gradation from normal pairing to a complete failure. Circles represent chromosomes, white ones being those confined to the male sex (the "Y" set); the *X* chromosome is contributed to the female progeny. In *Llaveia* there is 95 per cent. of normal pairing, 5 per cent. of failure of one pair. There is probably no differentiation between the pairing chromosomes. In *Protortonia* only two chromosomes pair and these are perhaps differentiated. In *Gossyparia* there is no pairing and half the sperm degenerate. *Icerya* is haploid in the male tissue. (From F. and S. H. Schrader, 1931.)

chromosomes separate from the rest at the second division, which is otherwise abortive. Thus four nuclei are formed with the haploid number of chromosomes, and if it were possible to consider these as of two alternative sex types, the precocious chromosomes representing those characteristic of the male, the " *Y* " set, and those that are homozygous in the female, the " *X* " set, it would be easy to see in *Gossyparia* an exaggeration of the differentiation of *Pseudococcus* and *Protortonia*. But Schrader (1929) finds that half the sperm die, and considers these to be of one type, the " *Y* " set. If this is so, obviously the chromosomes that are lost in the degenerating sperm of one male are precisely those that were not lost in its own male parent. Moreover, since the half that survive must contain both male-determining and female-determining chromosomes, these must have been derived in part from opposite parents. This upsets the notion of the constancy of behaviour being due to any properties inherent in the chromosomes concerned. The view that the sperm which die contain what they describe as the " degenerate " set of chromosomes is held by the Schraders (1931) to be the most decisive evidence in favour of the theory that this set is " progressively degenerating," but it seems rather to be the chief obstacle to regarding the series of steps as progressive.

If it were possible to assume that the sperm which survived carried both kinds of chromosomes the series could be taken to show a progressive change, and this would be the means by which the whole of one set might be lost in the same way and for the same reason as the *Y* chromosome has been lost in the Orthoptera and elsewhere. Hence the haplo-diploid system of sex-differentiation, which is found in yet another coccid, *Icerya purchasi*, might arise (*v.* diagram). Another possible method of origin is described later (Ch. XVI). The two seem equally plausible, and the possibility that the same system has arisen in different ways need not be dismissed.

Note. The observations on spermatogenesis in *Sciara* show remarkable abnormalities which possibly have a wider significance. Their interpretation is, however, still uncertain (*v.* Metz *et alii*). Similarly, " brachymeiosis " in the Ascomycetes cannot yet be related to other types of nuclear division (*v.* Gwynne-Vaughan and Williamson, 1931 ; *cf.* Wakayama, 1930).

CHAPTER XIV

PERMANENT DIPLOID HYBRIDS

Conditions of Permanence—The Sex Heterozygote—Sex Chromosomes—Pairing and Segregation—Differentiation and Genetic Properties—The Complex Heterozygote—Inheritance and Mutation in Œnothera—Its Chromosome Basis.

1. INTRODUCTION

Two kinds of heterozygote exist in which the difference between the gametes is deeper and broader in effect than the simple differences shown by mendelian and simple structural hybrids, but in which the segregation is mendelian : the difference behaves as a unit and only two types of gamete are normally produced. These properties are correlated with permanence ; that is to say, the heterozygous condition is the property of the whole race or of a necessary part of it.

The first type is the " complex heterozygote," typically seen in many *Œnothera* species. These species breed true to their heterozygous condition owing to their producing only two kinds of gamete and owing to the homozygous form of either type being inviable.

The second is that found in organisms with hereditary sex determination (Ch. I). In these, where the differentiation of the sexes is in the diploid phase, one sex is homozygous for the sex determinants, the other heterozygous. The heterozygous sex can be shown genetically to produce two kinds of gametes, one the same as that of the homozygous sex, the other different ; they therefore give the opposite sexes on fusing with the one kind of gamete produced by the homozygous sex. The heterozygous sex may be the male or the female. Where, on the other hand, differentiation is in the haploid phase the diploid asexual generation is heterozygous in sex determinants and gives the two sexes in equal numbers. The heterozygous condition is therefore essential for differentiation by

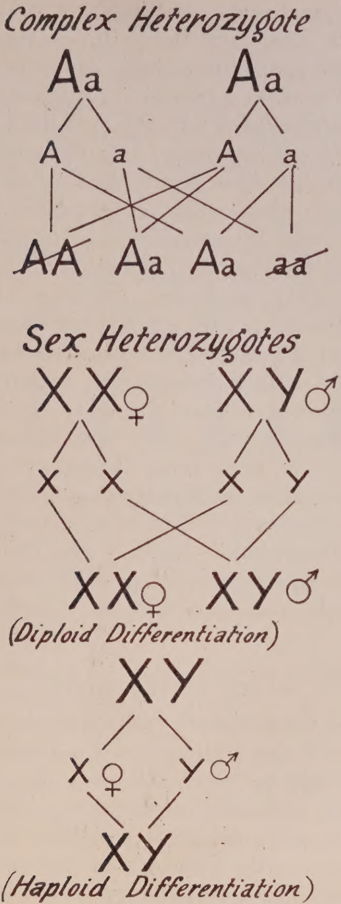

Complex Heterozygote
Aa Aa
A a A a
AA Aa Aa aa
Sex Heterozygotes
XX♀ XY♂
X X X Y
XX♀ XY♂
(Diploid Differentiation)
XY
X♀ Y♂
XY
(Haploid Differentiation)

FIG. 95.—Scheme of inheritance in complex and sex heterozygotes showing that elimination of homozygotes in the one and the exigencies of reproduction in the other secure permanence in the system.

genetic segregation, but has no necessary connection with one sex or the other. Whether the heterozygote is male, female or asexual is indifferent to the origin and working of the chromosome mechanism, which depends on the genetic reaction of the original sex factors and the relative importance of the haploid and diploid generation. It is therefore convenient in considering the mechanism to speak of sex-heterozygotes rather than of the heterozygous sex.

As in the complex heterozygote, so in the sex-heterozygote, the differences (which determine sexual differentiation) behave as a unit in inheritance. The sex heterozygote differs in that one of its zygotic types can exist in a condition that is homozygous so far as the sex differences are concerned and show free segregation of all differences found in that condition. Permanence is secured by the complementary functions of the sexes in reproduction.

The two types of heterozygote have in common the two properties of permanence and unity in inheritance. Clearly the permanence could not be preserved without the unity, nor could differences more complex than any that have been known to arise singly have developed as a unit except through an accumulation of changes such as requires permanence in the system accumulating them. The one essential for these combined properties is a suppression of crossing-over between the differences that are accumulated. Bearing in mind this principle we shall now examine the evidence of the development of the two kinds of permanent hybrid.

2. SEX HETEROZYGOTES

(i) **Types of Sex Chromosomes.** The sex heterozygote is usually the male. Only in the Lepidoptera, the birds and some fishes, amongst animals, and in *Fragaria* (Kihara, 1930 *a*) among plants is the female known to be the heterozygote. With haploid sexual differentiation, in some of the Bryophyta, the diploid asexual sporophyte is necessarily heterozygous and corresponds in its genetic properties with the sex heterozygote elsewhere.

At meiosis in the sex heterozygote of animals and plants two kinds of gametes must be supposed to be produced on genetical grounds. Cytological observation shows in almost all such organisms that the first division separates groups differing in regard to one or more chromosomes—the *sex chromosomes*. The chromosome or chromosomes which correspond with those found in the homozygous sex are called *X* chromosomes, their mates, *Y* chromosomes. In the simplest type there is one *X* and one *Y* chromosome. The other chromosomes in which both sexes are equally homozygous are known as the *autosomes*. The types of differences between *X* and *Y* chromosomes, as seen at mitosis, may be classified as follows :—

1. Organisms in which the *X* and *Y* chromosomes are not structurally distinguishable (*e.g.*, *Oncopeltus*, Wilson, 1912; *Drosophila Willistoni*, Metz, 1926) or scarcely so (*e.g.*, *Nezara*, Wilson, 1905, 1911). In *Drosophila obscura* two races exist, one with similar *X* and *Y* chromosomes, the other, the commoner type, with a smaller *Y* chromosome (Lancefield, 1929).

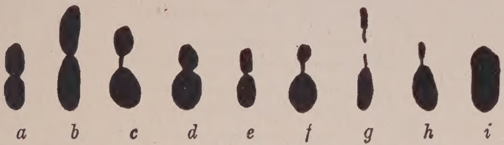


FIG. 96.—The *X* chromosome (below) and the *Y* (above) paired end-to-end at meiosis (first or second metaphase) in the heterozygous sex in various insects (after Wilson and Stevens) showing the transition from equality in size to the disappearance of the *Y*. *a*, *Oncopeltus fasciatus*. *b*, *Nezara hilaris*. *c*, *Lygæus bicrucis*. *d*, *Euschistus fisilis*. *e*, *Thyanta custator*. *f*, *Lygæus turcicus*. *g*, *Nezara viridula*. *h*, *Trirhabda*. *i*, *Protenor belfragei*. (From Witschi, 1929.)

2. Organisms in which the *X* and *Y* chromosomes differ more or less considerably. Every gradation is found between the slight difference in *Drosophila melanogaster* (Fig. 14) and the considerable difference in *Sphærocarpus Donellii* (Lorbeer, 1927, 1930), and in man (Evans and Swezy, 1930). The *X* chromosome may be the largest member of the complement (as in *Sphærocarpus Donellii*; *Leptophyes*, Mohr, 1916; *Phragmatobia fuliginosa*, *Gryllus campestris*, Ohmachi, 1923, and *Humulus japonicus*) or the smallest (as in *Asilus notatus*, Metz and Nonidez, 1923, and *Macropus*, Agar, 1923). The *X* chromosome is usually larger than the *Y*, but is occasionally smaller (as in *Drosophila melanogaster*).

3. Organisms in which the *Y* chromosome is represented by two

or more fragments. The mode of origin of this type from the first is made clear by Seiler's work on *Phragmatobia fuliginosa* (1925). Two geographic races exist, one of which has two pairs of small

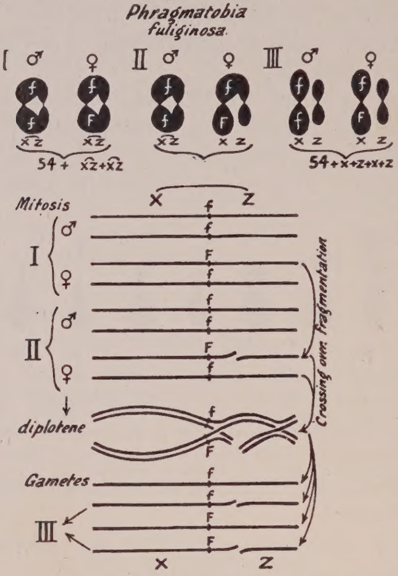

Phragmatobia fuliginosa.
I ♂ ♀
II ♂ ♀
III ♂ ♀
f f f F f f f F f f F
xz xz xz x z x z x z
54 + xz+xz
54+x+z+x+z
Mitosis
X f Z
I ♂ ♀
II ♂ ♀
diplotene
Gametes
III
Crossing over Fragmentation
X Z

FIG. 97.—Diagram showing how fragmentation in a chromosome carrying sex factors makes the sex chromosomes distinguishable in the heterozygous sex and how crossing-over between the point of breakage and the sex-factors destroys the distinction. I, the unfragmented type with $54 + X + Y$ chromosomes in the female. II, breakage of the Y chromosome into two components, "X" and "Z," "X" containing the F factor or factors. Crossing-over in this female in the X and Y chromosomes between the breakage and the F factor will give the diplotene configuration shown and yield males with a fragmented X chromosome, *i.e.*, type III. The female is heterozygous in the Lepidoptera.

chromosomes instead of one large pair found in the other. A third race is found in which the males have the single large pair while the females have one large chromosome associated with two small ones (*v.* Ch. V). Evidently therefore the sex factors are located in

PLATE VII

FIGS. 1–5.—Meiosis in *Phragmatobia fuliginosa*, Lepidoptera. (From Seiler, 1925.)

Fig. 1. Fragmented race, male, $n = 29$. Fig. 3. Fused race, male, $n = 28$. Figs. 2, 4 and 5. Hybrid between the two races, male, showing pairing of two small chromosomes with one large one.

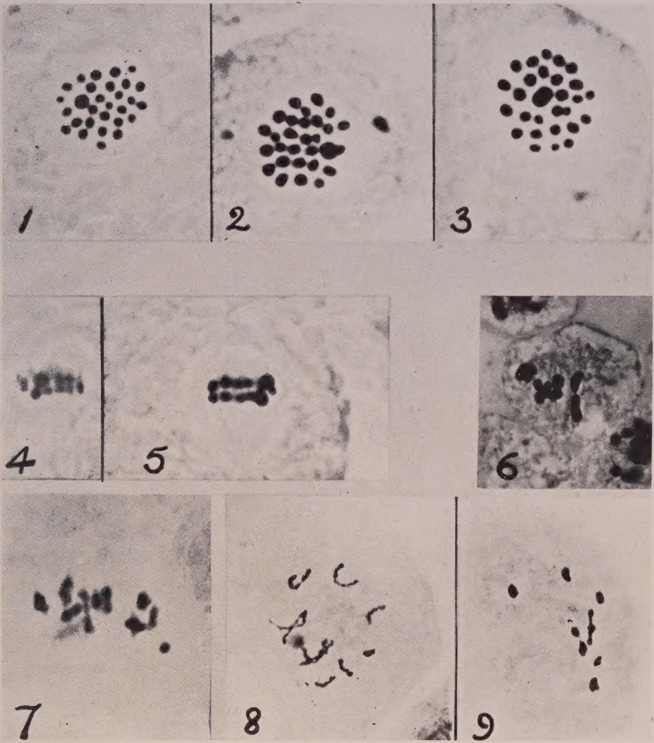
FIG. 6.—First metaphase in *Melandrium album*, male: pairing of X and Y. (From Belar, 1925.)

FIG. 7.—First metaphase in *Zea Mays*, monosomic shoot of a diploid plant, showing 9 bivalents and 1 univalent. × 650. (From McClintock, 1929 *b*.)

FIGS. 8 AND 9.—Polymitosis in *Zea Mays* pollen grain.

Fig. 8. Late prophase. Fig. 9. Metaphase. Two chromosome pairs, probably with interstitial chiasmata in each nucleus. (Reproduced by kind permission of Dr. G. W. Beadle.)

PLATE VII



[*To face p.* 380.

this group. Although the third race might have arisen as a cross from the first two it may equally be regarded as an intermediate stage in the change from the one type to the other, for, in the absence of crossing-over, fragmentation in the *Y* of the large chromosome type will lead to the intermediate type. Only if crossing-over occurs between the sex factors and the point of breakage will the intermediate type yield the small chromosome type. Evidently such crossing-over has taken place. This example therefore provides a diagrammatic illustration of the relationship between crossing-over and the preservation of differences between sex chromosomes (*v.* Fig. 97).

Similarly, in species of *Anisolabis* and individuals (probably races) of *Forficula auricularia* (Whitney, 1928) the *X* chromosome is broken in two as the *Y* is in *Phragmatobia*. A triple chromosome is formed at meiosis, probably also by the pairing of each component of the *X* with the corresponding part of the *Y*. The pairing of one of the components occasionally fails, just as in ring-forming organisms the ring is replaced by one or more chains. Other races of *F. auricularia* have the two *X* components permanently fused.

The triple chromosomes found in the sex heterozygote in *Tenodera superstitiosa* (Oguma, 1921, *cf.* Wilson, 1925, Fig. 373), *Humulus japonicus* (Kihara, 1929 *a*; Winge, 1929; Sinoto, 1930), *Rumex acetosa* (Kihara and Ono, 1925; Sinoto, 1930) have probably arisen as indicated in *Phragmatobia*. They are therefore (apart from other differences) either *fragmentation* or *fusion heterozygotes*.

Winge's suggestion (1929) that the chain of three chromosomes in *Humulus japonicus* consists of three identical *X's* is inconsistent with (i) the observation of differences between them in somatic mitosis (Kihara, 1929 *a*); (ii) the failure to observe the other three characteristic types of normal trivalent at meiosis; (iii) the observation of a chain of five in one individual (*v. infra*); (iv) the genetic principles of sex determination in other plants and animals.

4. In *Humulus japonicus* (Kihara, 1929 *b*) and *H. lupulus* (Sinoto, 1930) a further structural change has occurred in the extension of the differences in the sex-heterozygote to another pair of chromosomes, while the homozygous sex presumably continues to have simple pairs (Fig. 98). A race of *Humulus lupulus* has a

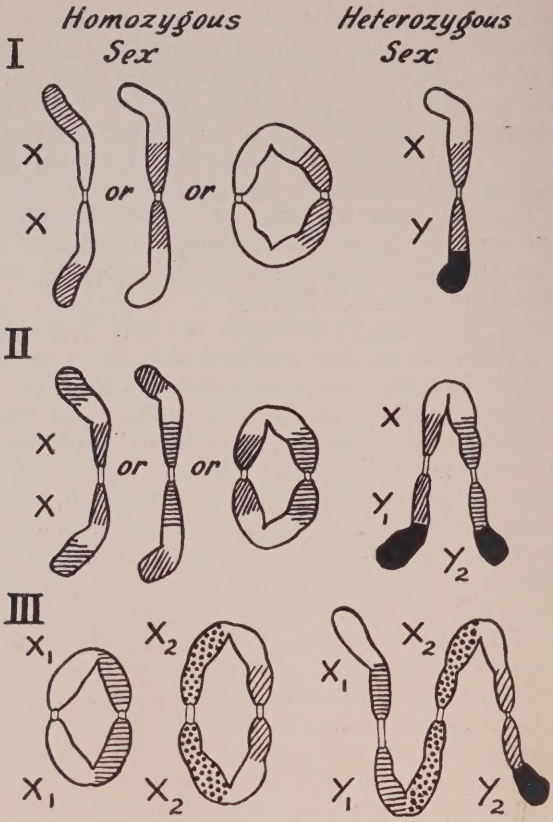

Homozygous Sex
Heterozygous Sex
I
X
X
or
or
X
Y
II
X
X
or
or
X
Y_1
Y_2
III
X_1
X_2
X_1
X_2
X_1
X_2
Y_1
Y_2

FIG. 98.—Pairing of chromosomes in the two sexes showing parts of X and Y that are homologous similarly hatched and stippled, parts of X that are not represented in Y blank, and parts of Y not in X black. I, *Humulus lupulus*, simple type. II, *H. japonicus*, simple type (fragmentation heterozygote). III, *H. lupulus*, with male as interchange heterozygote having X_1, Y_1, X_2 and Y_2 chromosomes, corresponding to segments BXA, AQ, QP, PY (*cf.* text). *Note.*—Types I and II are common in plants and animals. The spindle attachment being median in the X_1 the two X chromosomes in the homozygous sex can form chiasmata in one or both arms to give a rod or a ring. From type II the chain of five is derived as the chain of four is derived from type I.

chain of four instead of one unequal pair and an individual of *H. japonicus* has been found with a chain of five instead of a chain of three. Each of these modifications can be supposed to be derived from the simpler type by segmental interchange between sex chromosomes and autosomes in the same way as a ring of four is presumed to be derived from two pairs in ordinary interchange heterozygotes. Thus, if the three sex chromosomes of the simpler form of *Humulus japonicus* are composed of segments (homologues having the same letters):

$$YA\text{–}AXB\text{–}B$$

then segmental interchange between YA and an autosome PQ, giving two new chromosome types YP and QA, will form a chain of five in the interchange-cum-sex-heterozygote, thus:

$$YP\text{–}PQ\text{–}QA\text{–}AXB\text{–}B\,;$$

this will yield two types of gametes YP, QA, B and PQ, AXB. The homozygous sex will be unaltered by the change, still having the composition:

$$PQ\text{–}QP,\ AXB\text{–}BXA.$$

The origin of the chain of four in *H. lupulus* differs from this in their being no " B " chromosome.

The sex heterozygote is therefore, apart from other differences, an interchange heterozygote, and the mechanism combines the usual sex mechanism with that in the complex heterozygotes to be considered later. This second instance of the preservation of a demonstrable form of structural hybridity by the sex heterozygote shows the essential similarity between the complex and sex heterozygote.

5. Even more complex conditions are found in *Blaps lusitanica* (Nonidez, 1920) and in various Hemiptera and Nematoda. In these the X chromosome is represented by several separate bodies in somatic cells. They unite at meiosis, and pair also with the Y chromosome. It would seem that this fusion has nothing to do with normal meiotic pairing, since it cannot be supposed to be determined by the homology of the elements that associate. It is, on the other hand, of the same kind as a temporary fusion between what are evidently non-homologous chromosomes at meiosis in both sexes in

Lymantria monacha (Seiler and Haniel, 1921). The haploid number of *Lymantria dispar* and *L. japonica* is 31, that of the comparable species, *Phragmatobia fuliginosa* 28, including one large chromosome which contains the sex factors, and is fragmented in some races (*v. supra*). Evidently, therefore, three chromosomes of the one species have permanently fused in the other, or one in the other has permanently fragmented into three. In *Lymantria monacha* 62 chromosomes are seen at the somatic divisions but only 28 bodies at the second meiotic division, and also at the first in the male; 31 bodies are seen at the first division in the female. Such a fusion as has proved permanent in the other species can apparently be determined temporarily by developmental conditions, which differ in this respect in the two sexes, in *Lymantria monacha* (*cf.* Ch. III).

6. The variation which occurs in the relative size of the X and Y chromosomes might be supposed to have two extremes, the complete disappearance of one or the other. But the X chromosome never disappears. That is to say, the distinction between the sexes never consists in the presence of a single supernumerary chromosome in one sex which is not represented in the other. The opposite extreme, in which the Y chromosome has disappeared, is very common in animals, *e.g.*, Orthoptera, Hemiptera, Coleoptera and Nematoda. The sex chromosomes are said to be of the XO type. The random segregation of the single X chromosome gives two classes of gametes with different numbers of chromosomes. These can be distinguished in the living sperm of the nematode *Ancyracanthus* (Mulsow, 1912), and the direct connection therefore established between segregation and sex determination. The X chromosome (as in the XY type) may have several independent components (*e.g.*, *Perla marginata*, Neuroptera). These may fuse temporarily at meiosis (*e.g.*, Nematoda and Aphides, Morgan, 1912). In *Perla* they fuse at diakinesis, but are independent at metaphase. They nevertheless pass to the same pole. This suggests that in all cases of unpaired sex chromosomes one pole has a definite attraction for the sex chromosome or a greater attraction than the other pole and that the segregation is not purely a matter of chance (*v. infra*).

7. This last type may give a secondary XY mechanism owing to

the fusion of the *X* chromosome with an autosome, giving an unequal pair at meiosis (de Sinéty, 1901; McClung, 1905, 1914, 1917 in Orthoptera). The origin of this type is betrayed by its prophase behaviour. The attached *X* chromosome condenses in advance of the autosomes, and is therefore distinguishable from them until metaphase. Some species are constant in having the attachment of the *X* (*e.g.*, in *Leptynia* and *Mermiria*) others have races with the free *X* and races with the attached *X* (*e.g.*, in *Menexenus* and *Hesperotettix*, *cf.* Fig. 37).

Such a fusion has probably taken place in *Ascaris megalocephala* (Edwards, 1910; Geinitz, 1915) for male individuals occur with a single *X* chromosome separate instead of included in the ordinary compound chromosome. In the male *Macropus* (Agar, 1923) the special behaviour of the two elements which condense precociously at meiosis shows them to be *X* and *Y* chromosomes. But the *X* chromosome is permanently fused with an autosome in both sexes. A configuration consisting of three unequal chromosomes is formed at meiosis and segregates like that in *Tenodera* and *Rumex*.

That a change of this type, although translocation rather than fusion, has been effective in *Drosophila* is indicated by a comparison of linkage maps and chromosomes in *D. melanogaster* and *D. Willistoni* (Lancefield and Metz, 1922). The sex chromosomes of the latter species are V-shaped, while one pair of autosomes are rod-shaped. The reverse is the case in *D. melanogaster* (Fig. 14). One arm of the *X* chromosome of *D. Willistoni* corresponds with the *X* chromosome of *D. melanogaster* in the linked factors located in it (*cf.* Koller, 1932 *b* on *D. obscura*).

The following list gives the most satisfactory observations of sex chromosomes in plants, in which the chief recent advances have been made.

There are other observations of unequal chromosomes in diœcious plants, but whether these chromosomes are concerned with sex determination is doubtful. Proof is beset with even more difficulty in plants than in animals on account of the prevalence of polyploidy and hybridisation and the absence of precocity. Multiple chromosomes in *Rumex acetosella* (6*x*) are probably merely the normal associations of homologous chromosomes in a polyploid, or,

TABLE 57

Sex Chromosomes in Plants

	Chromosome Formula of Heterozygote.	Authority.
*Sphærocarpus Donnellii** .	$14 + XY$	Allen, 1917. Wolpon, 1925. Lorbeer, 1927, 1930.
Melandrium album .	$22 + XY$ ♂	Blackburn, 1924. Winge, 1923 *b*. Meurman, 1925. Belar, 1925.
M. rubrum . . .	,,	Blackburn, 1924. Meurman, 1925.
M. divaricatum . .	,,	Blackburn, 1928.
M. glutinosum . .	,,	
Humulus japonicus . .	(i) $14 + XY_1Y_2$ ♂	Kihara, 1929 *a*. Tuschnjakowa, 1929.
	(ii) $12 + A_1A_2XY_1Y_2$ ♂	Kihara, 1929 *b*.
H. lupulus . ..	(i) $18 + XY$ ♂	Winge, 1929.
	(ii) $16 + A_1A_2XY$ ♂ or $16 + X_1X_2Y_1Y_2$ ♂	Sinoto, 1930.
Rumex sect. *Acetosa* (8 species) . . .	$12 + XY_1Y_2$ ♂	Kihara and Ono, 1925. Ono, 1930 *b*. Sinoto, 1930. Meurman, 1925. Kihara and Ono, 1928. Jaretsky, 1928. Takenaka, 1930.
Empetrum nigrum . .	$24 + XY$ ♂	Hagerup, 1927.
Fragaria elatior . .	$40 + XY$ ♀ ($6x$)	Kihara, 1930.

* *Cf.* also *Pogonatum inflexum*, Shimotomai and Koyama, 1932.

where eight chromosomes are associated, the result of interchange hybridity (Ch. V). Unequal chromosomes in *Populus* and *Salix* may be expected from the frequency of hybrids in these genera, and their presence is inconclusive (Blackburn and Harrison, 1924; Meurman, 1925; Harrison, 1926; Erlanson and Hermann, 1927). The illustrations of *Elodea* (Santos, 1923, 1924) and *Silene Otites* (Blackburn, 1928) are indecisive. Hagerup's observation (1927) of XY pairs in the tetraploid *Empetrum hermaphroditum* (corresponding with those in the diploid relative) is improbable on genetical grounds, while XX and YY pairs are more probable on cytological grounds on account of differential affinity. Differentiation of sex chromosomes has not therefore been proved in any polyploid species but *Fragaria elatior*. Where it arises it will not appear as a derivative of a diploid system, for a new polyploid will only maintain itself at the outset if hermaphrodite ; and it will be likely to breed true to hermaphroditism. There is nothing, however, to prevent differentiation arising *de novo* in an established polyploid, as it doubtless has arisen in *Fragaria elatior*.

(ii) **Pairing of Sex Chromosomes.** In the heterozygous sex, where there are dissimilar sex chromosomes (*X* and *Y*) derived from opposite parents their behaviour at meiosis corresponds with what we are led to expect. At metaphase they are always paired end to end. At prophase there is every degree of closeness in association corresponding with increasing degrees of differentiation in the following ways :—

(*a*) In the flowering plants and in some animals pairing between the chromosomes is almost normal. This corresponds with Winge's observation that crossing-over may take place between them (*Lebistes*, 1923 *a*, 1930 ; *Melandrium*, 1931). In the homopteran *Enchenopa binotata* (Kornhauser, 1914) the *X* and *Y* chromosomes associate at both ends, although probably not in the middle at pachytene. The *Y* chromosome being longer the pair is bent into an arc. Apparently a chiasma is established near one end and a rod bivalent results. This is probably the type of pairing between *X* and *Y* chromosomes that are moderately differentiated, as in various mammals (Minouchi, 1929, 1930).

(*b*) In Coleoptera (*cf.* Nonidez, 1920) and some Mammalia (*cf.* Agar, 1923 ; Painter, 1924, 1925) the *X* and *Y* chromosomes are united throughout the prophase (after pachytene) but show strong precocity (Ch. IX).

(*c*) In many Hemiptera, *e.g.*, *Lygæus*, *Oncopeltus*, etc. (Wilson, 1909, 1912), the *X* and *Y* chromosomes may or may not meet at pachytene, in others (*Brochymene*, Wilson, 1905 *a*) they regularly meet. If they meet they fall apart again at diplotene (*i.e.*, they form no chiasma), divide equationally at the first division, and segregate after momentary touching of their daughter halves end-to-end at the second division. This extreme of differentiation is found in *Oncopeltus*, where no size difference is observed between the chromosomes, thus showing that mere loss and gain is only one of the kinds of structural change that may arise to distinguish the sex chromosomes.

These observations suggests that the segments of the differential chromosomes which retain their homology are their distal ends. Presumably the terminal metaphase association which develops from pachytene is due to terminalisation of interstitial chiasmata, while the momentary metaphase pairing is due to an attraction between small terminal segments that are homologous (Ch. XII). Where the attachment constriction of the X chromosome is terminal it can therefore only be expected to pair at one end to give the simple XY type; where it is median (either originally or following fusion with an autosome) the XY_1Y_2 type is rendered possible. The position of the attachment constriction will therefore condition the type of mechanism developed where terminalisation occurs.

Interstitial chiasmata have not as yet been seen between X and Y chromosomes. They have been observed between autosomes to which an X chromosome is attached (as in *Leptynia*, Sinéty, 1901). The possible exception to this is Tuschnjakowa's observation in *Humulus japonicus* (1929 *b*, 1930) which does not agree with that of other workers. This is probably accounted for by her material, which is derived from inter-racial crossing, and may have an exceptional and unstable relationship between the sex chromosomes.

(iii) **Segregation of Sex Chromosomes.** Paired sex chromosomes separate at the first division. Unpaired sex chromosomes are a permanent property of the race and behave regularly (unlike the unpaired chromosomes of adventitious hybrids) in one of the following ways :—

(*a*) In the Orthoptera, the unpaired X chromosome (which is precocious during prophase) lies to one side of the equator and passes, without division, before the paired chromosomes to the nearer pole. It then divides at the second division.

(*b*) In the Aphides (Morgan, 1912, 1915) and Nematoda (Mulsow, 1912) it lags behind the bivalents, but otherwise behaves in the same way.

(*c*) In some Hemiptera (*Vanduzea arcuata*, and species of *Ceresa*, Boring, 1907), the unpaired X chromosome may pass to the pole either before or after the autosomes.

(*d*) In other Hemiptera (*Lygæus*, Wilson, 1905 *a*) the X and Y chromosomes are unpaired at the first division but regularly lie on the equator and divide when the bivalents separate. Their halves then pair, end-to-end, at the second division and pass to opposite poles. This pairing is perhaps due to a property analogous to terminal affinity (*cf.* Ch. XII).

(*e*) An unpaired X chromosome is known to divide equationally at the first division in a few species and pass to one pole at the second division (*Photinus consanguineus* and *P. pennsylvanicus*, Coleoptera, Stevens, 1909 *a* ; *Anasa tristis*, Wilson, 1905 *b* ; *Alydus* Hemiptera, Reuter, 1930).

Since only a part, and often only a small part, of the X chromosome can be supposed to correspond exactly with material in the Y chromosome, it is clear that the mechanism of chiasma formation, or whatever substitute for chiasma formation is effective in pairing will not be able to secure the same regularity in pairing as in the autosomes. Such is the case as shown both by direct observation and inference from the occurrence of " non-disjunction " in genetical experiments. The dissimilar sex chromosomes occasionally fail to pair in the following species in the heterozygous sex :—

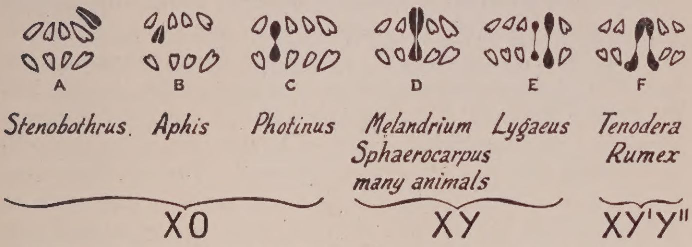


FIG. 99.—Diagram showing the methods of segregation of sex chromosomes at the first anaphase normally occurring in different species.

Fragaria elatior, ♀ (XY)	Kihara, 1930.
(also a pair of autosomes may fail)	
Forficula auricularia ♂ (X_1X_2Y) . .	W. P. Morgan, 1928.
Anisolabis annulipes ♂ (X_1X_2Y) . .	

Humulus lupulus ♂ (chain of four)	Sinoto, 1930.
Mus musculus ♂ (XY) (particularly in waltzing strain, which is probably of hybrid origin)	Painter, 1927.

Where pairing fails, the unpaired chromosomes may divide at the first division (*e.g.*, in *Fragaria*), but will in any case be distributed amongst the four daughter-cells at random with regard to one another. Some will therefore have both the X and the Y chromosome. This result has been referred to in *Drosophila* (*cf.* Stern, 1929 *a*) as following non-disjunction, but is, as we now see, often more properly to be ascribed to non-conjunction, *i.e.*, failure of pairing.

True non-disjunction is, however, regularly found with multiple chromosomes, especially the chains of three and four chromosomes found in *Humulus* and *Rumex*. To give the normal sex segregation, successive chromosomes must pass to opposite poles, so that half the gametes have the X chromosome and half the Y chromosomes (Fig. 98). This segregation occurs in 85 per cent. of mother-cells in *Humulus japonicus* (according to Sinoto). The non-disjunction is due to the same cause, irregular orientation of the chain at metaphase, and has the same effect, the formation of gametes with too many and too few chromosomes, as non-disjunction in other cases of diploid ring and chain formation in interchange heterozygotes (*cf.* Sinoto, 1930 ; Winge, 1929 ; Kihara, 1929 *b*).

(iv) Note on Genetics of Sex Determination. In any species where the chromosomes of the two sexes differ in size the sex differentiation can be seen to follow from the segregation of dissimilar chromosomes at meiosis. In some species (as shown in *Ancyracanthus* by Mulsow) every step in development can be seen, from the act of unequal segregation to the differentiation of the sex types which is invariably correlated with it. This gives us the minimum information with the maximum certainty. It shows us the mechanism underlying sex determination, but it does not show us how the mechanism arose or how it operates. There are therefore an evolutionary and a physiological problem to be decided. Both have to be approached by the comparative method.

The evolutionary problem has been approached by attempting a unitary theory of sex determination. Correns (1928) considers that such a theory may rest on the assumption that homologous genes are present in all species for sex differentiation at each stage of the life cycle, and that allelomorphs of these affecting one stage are found in one group and affecting another stage in another group (*cf.* also Allen, 1932). This hypothesis is of little value. The assumption of genes in one organism affecting differences only found in an entirely different group of organisms depends on assumptions of the nature of variation for which there is no evidence. Sex differentiation has certainly arisen independently in different groups. The fact of its analogy of mechanism is only due to the inevitable limitations of its mechanism—segregation of alternatives at meiosis.

The second attempt is based on the study of sex conditions in hybrids. In these, sex seems to be determined by the balance of two opposing tendencies—to maleness and to femaleness. They can be represented more or less quantitatively. The one tendency is determined by the *X* chromosome, and is therefore present in a single dose in one sex, in double dose in the other. The opposite tendency is determined by the autosomes (or the *Y* chromosome in *Lymantria*) and is in the pure species stronger than the single dose of *X*, but weaker than the double dose. When races or species are crossed this relationship does not hold, and intersexes result. This formula may be taken as an approximate description of the differences between races and between the effect of the *X* and of the other chromosomes. They may be expressed quantitatively and according to direction—male or female.

The formula does not, however, decide the question as to whether the effect is produced by differences in proportion or in summation, and a solution of this physiological problem is necessary before the evolutionary question can be more closely considered. This is provided by work on forms of *Drosophila* with different numbers of chromosomes.

Bridges (1922) found that, in the progeny of triploid females of *Drosophila*, flies occurred having different numbers of *X* and *Y* chromosomes and autosomes (Chs. II, III and IV). Some of these were sterile, but the whole of the types found might be arranged in a more or less linear series from forms of male character to others of female character, through normal sexual types and intersexes. The extreme types at both ends were sterile and were described as super-males and super-females; so also were those apparently normal males which had no Y chromosome (presumably through lack of pairing of the X at meiosis). The succession in this series was found to be related to the proportions in which the autosomes and the X chromosome were present, and entirely unrelated to the presence of the Y. Thus if the autosome complement is denoted by A, the series (*cf.* Fig. 14):—

$$AAAX(Y),\ AAX(Y)\ \text{♂},\ AAAXX(Y)\ \left\{\begin{array}{l} AAAXXX\ (3x)\ \text{♀} \\ AAXX\ (2x)\ \text{♀} \\ AX\ (x)\ \text{♀} \end{array}\right.\quad AAXXX$$

represents the transition from "super-male" to "super-female." Haploid patches of tissue (AX) in mosaics have since been found to be female in character as expected on this theory.

It is interesting to notice that types otherwise similar are more female with the higher number of fourth chromosomes. The fourth chromosome therefore acts in the same sense as an X chromosome, and in the opposite sense to the other autosomes. This departure from the rule can be simply understood by supposing that the small fourth chromosome has arisen by fragmentation of the X, a not improbable origin on general grounds.

When the principles of proportion-adjustment or balance to be derived from the simpler study of trisomic plants are applied to an organism with alternative X and Y inheritance it is seen that two systems of adjustment must work in such an organism. X and Y must both be adjusted in proportion to the autosomes—as we have seen is the case, X having a resultant normal female effect, Y having a neutral effect. Further, both must be balanced. In the Y neutrality implies balance. In the X recent work has indicated an internal differentiation. Certain fragments of the X which have a phenotypic effect on the males that bear them do not reduce their fertility (Muller, 1930 *a*), probably on account of a margin of safety, a threshold value, in the reaction of the normal type. When such fragments are added to intersexes they alter the sexual grade of the intersex in various degrees according to the fragment concerned (Dobzhansky and Schultz, 1931). These effects can be expressed more or less quantitatively as Goldschmidt has supposed. At the same time the X is shown to be differentiated and adjusted, *i.e.*, balanced.

Proportion can be shown to be important in sex determination in other organisms. Triploids and tetraploids in *Rumex Acetosa* and *R. montanus* of the constitutions: $18 + 2X + Y_1Y_2$ and $24 + 3X + 2Y_1Y_2$ are intersexual (Ono and Shimotomai, 1928; Ono, 1930), but whether those lacking Y_1 and Y_2 are also intersexual (as they would be on the *Drosophila* system) is not yet known. Forms with an abnormal (probably deficient) autosome have, however, been found, and they, although diploid, are slightly intersexual (Ono, 1930). Hermaphrodites in *Melandrium album* have the male complement (Belar, 1925), while those in *M. rubrum* have the female complement (Åkerlund). These results indicate one essential conclusion (which is in accordance with genetic evidence): the autosomes are not without influence in sex determination. A mutation affecting sex has been found in an autosome of *Drosophila simulans*.

The quantitative theory of sex, derived from the study of gene differences in hybrids, and the proportion theory derived from the study of proportion differences in polysomic forms answer different questions. The one shows how gene differences arise (and act), and the other shows how they interact. Both provide the basis on which a unitary theory may rest. The cytological evidence, on the other hand, reveals a third point of view—the evolutionary one. This will now be considered.

(v) **The Differentiation of the Sex Chromosomes.** The complex genetic differences between the sexes lead us to expect complex differences between their chromosomes such as are actually to be seen either in their form or in their relative behaviour at meiosis. Experience elsewhere points to these differences being largely due to structural change, and many observations bear witness to the importance of such change in the development of the sex chromosomes, *e.g.*, fusion in *Mermiria*, fragmentation in *Phragmatobia*, *Metapodius*, and *Alydus*, translocation in *Drosophila obscura*, interchange in *Humulus*.

The question then arises as to how a group of differences can act as a permanent unit in inheritance since crossing-over is a general property of pairing chromosomes (*v*. Chs. IX and XI). The most obvious explanation is that the sex factors arise in association with structural changes. Small relatively translocated segments evidently have little chance of crossing-over. This hypothesis is an expression in cytological terms of Muller's suggestion (1918) that the differences between complexes in *Œnothera* and between *X* and *Y* chromosomes in the sex heterozygote were due to the association of lethal factors with crossing-over suppressors. We now know that structural changes may combine these two functions (of which the first is largely superfluous in sex differentiation). However, a variety of evidence indicates that structural changes have not been the primary agent in the suppression of crossing-over and the conditioning of differentiation.

Suppression of crossing-over might equally be supposed to be genetically determined. This suppression would permit the development of structural differences which would themselves secondarily prevent crossing-over. The evidence that this is the origin of differentiation is both genetical and cytological, as follows :—

(i) Precocity of the sex chromosomes combined with pairing by terminal affinity, or precocity of parts of them, leading to localisation of chiasmata and crossing-over, is a reaction of the chromosomes to a genetic property of the organism. Localisation, for example, is found in *Fritillaria Meleagris*, but not in *F. imperialis*.

(ii) Abnormal forms of meiosis are characteristic of one sex in the Coccidæ and in *Sciara*, and affect equally like and unlike chromosomes. They must therefore be determined by a genetic property and not by hybridity as such.

(iii) Crossing-over is reduced in sex heterozygotes relative to the homozygotes in the autosomes as well as in the sex chromosomes. This points to a unitary and therefore genetic control of the difference (Haldane, 1922 ; *cf*. Huxley, 1928).

These remarks suggest the three means by which crossing-over may be suppressed, *viz.*, precocity, localisation and abnormal meiosis. The incidence of precocity and abnormal meiosis have already been discussed. Localisation is less easily detectable. It may be of two kinds. Most commonly sex chromosomes that appear to have paired normally during prophase are associated by terminal chiasmata at metaphase, as in all plants. In these the localisation must be near the distal ends of the chromosomes, and therefore terminalisation will occur rapidly and the original position of chiasmata will not be ascertainable. The differences will then

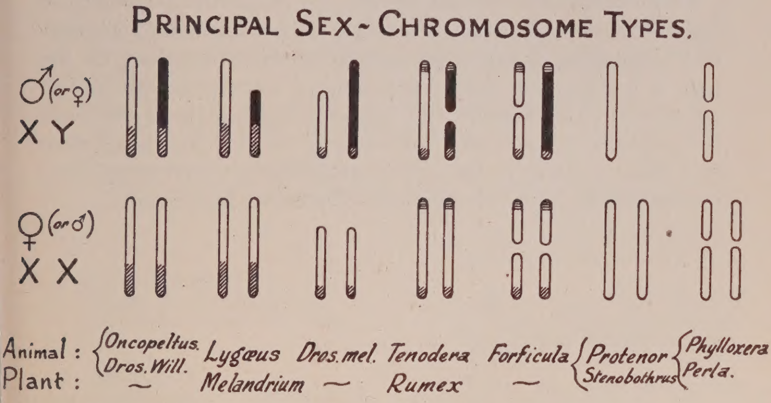
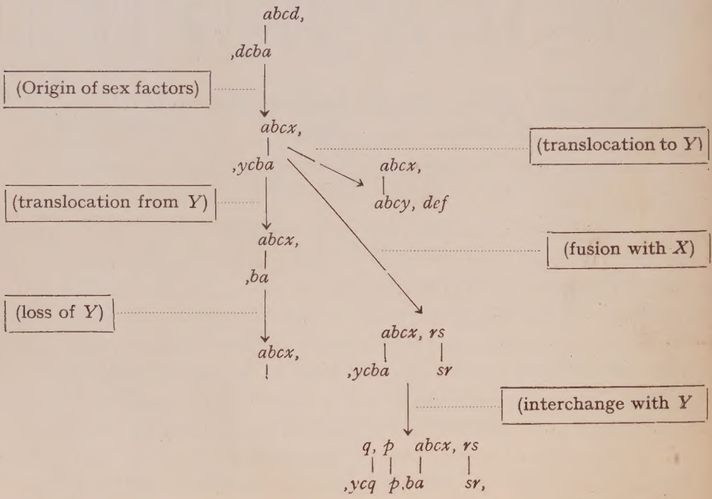

PRINCIPAL SEX-CHROMOSOME TYPES.
♂(or ♀)
X Y
♀(or ♂)
X X
Animal :
Plant :
Oncopeltus.
Dros. Will.
~
Lygæus
Melandrium
Dros. mel.
~
Tenodera
Rumex
Forficula
~
Protenor
Stenobothrus
Phylloxera
Perla.

FIG. 100.—Diagram showing the relationships of sex chromosomes in various types, using the same convention as in Fig. 98.

be proximal and the homologous parts terminal (*v.* Fig. 100). This condition is the same as that in the complex-heterozygote. A second possibility is that localisation occurs as in *Mecostethus* and *Fritillaria* in the neighbourhood of the attachment constriction. When this was median and both arms were differentiated, chiasmata with reciprocal cross-overs would need to be regularly formed to maintain the differentiation of the *X* and *Y* chromosomes. There is some reason to suppose that this system obtains in male *Drosophila* where all visible crossing-over is suppressed (D., 1931 *a*). The pairing of *X* and *Y* in trisomic forms indicates that they are homologous for only a short distance: they show differential affinity in XXY individuals. Where crossing-over in *Drosophila* is genetically reduced it is found to be concentrated nearer the spindle attachment (Ch. X). Reciprocal crossing-over is higher near the spindle than elsewhere (*cf.* Sansome and Philp, 1932), and is unduly frequent in the X chromosome (*cf.* Rhoades, 1931). The chromosomes seem to pair normally at zygotene and have interstitial chiasmata at metaphase (*cf.* Guyénot and Naville, 1930; Huettner, 1930). Further, the fusion of X and Y' chromosomes at the spindle attachment is perhaps related to crossing-over (Ch. X).

These observations do not exclude the alternative possibility of distal localisation, but they do exclude the possibility that crossing-over suppression is due to precocity or abnormal meiosis. On the type of crossing-over suppression adopted will depend the kind of differentiation produced. The following diagram shows the kinds of change that will give some of the results observed, with localisation in a distal segment *a* (the spindle attachment is represented by a comma and the series of differentiated particles by letters).


abcd,
,dcba
(Origin of sex factors)
abcx,
,ycba
(translocation to Y)
abcx,
abcy, def
(translocation from Y)
abcx,
,ba
(fusion with X)
(loss of Y)
abcx, rs
,ycba sr
abcx,
(interchange with Y
q, p abcx, rs
,ycq p.ba sr,

(vi) Conclusions. 1. Structural differences have arisen between chromosomes (X and Y) carrying opposite sex factors in the heterozygous sex by virtue of (i) preservation of the heterozygote by compulsory crossing in every generation ; and (ii) restriction of crossing-over between the sex factors and the structural differences. The differences arising in this way are analogous in mode of origin,

TABLE 58

Primitive and Advanced Types of Sex Determination

Rana-Lebistes-Melandrium-Rumex Type.	*Drosophila-Protenor-Lygæus* Type.
1. *Sex determination :* Partly by difference between XX and XY.	Purely by difference in balance between X/A and XX/A.
2. *Crossing over :* Occurs between some parts of X and Y and hence Y-linked factors occur.	Abolished between X and Y.
3. *Homologous parts of X and Y :* They are a considerable fraction and pairing is regular.	They are a small segment, indicated only by the "bobbed" allelomorph in Y. Occasionally they fail to pair and consequently both sex chromosomes pass to the same pole.
4. *Recessive factors in X :* Show in XY individuals in reduced effect (Winge, 1931).	Show in XY individuals in unreduced effect (*cf.* Muller, 1918), except "bobbed" in *D. melanogaster*.
5. *Related forms :* They are hermaphrodite (*Melandrium*, *Rana*) or have an opposite system of sex-determination (*Lebistes* and *Platypœcilus*).	They have the same system of sex-determination.
6. Intersexual forms appear in both types either through (i) gene mutation or hybridisation in the diploid or (ii) different proportions of the active chromosomes in polyploid and polysomic forms (*cf.* Belar, 1925 ; Winge, 1930 ; Ono, 1930 ; Bridges, 1923).	
7. *Variation in X and Y :* Still largely related on account of pairing and crossing-over. Hence size difference not extreme.	Independent. Hence size difference may be slight or extreme.
8. *Precocity of X and Y* Absent. Regular pairing in prophase.	Frequent. Pairing may be postponed to metaphase or telophase of the first division.

cytological basis and genetic effect to the complex differences in *Œnothera* to be considered later, and are unlike the differences usually subjected to mendelian analysis.

2. The restriction may apply to the whole chromosome complement (as suggested by the localisation of chiasmata and suppression of crossing-over applying to all the complement in some species), or merely to the sex chromosomes (as suggested by the precocity of these chromosomes at meiosis in many species, and by the possibility that their structural differences themselves inhibit pairing).

3. The initial stages of this differentiation are seen in the higher plants, where hereditary sexual differentiation has arisen recently, and independently in numerous genera, and probably in many species is not yet associated with any structural differences (although these may be present in the absence of size differences) and is nowhere conditioned by precocity of the sex chromosomes, except perhaps in the Bryophyta.

4. The final stages of differentiation are seen in animals in which the Y chromosome has disappeared or in which it has so little material in common with the X that it either rarely associates with the X at pachytene, or, if it does, fails to establish a chiasma, and consequently is only able to pair with it by a special mechanism of end-to-end association at metaphase.

5. The extreme stages of sex differentiation may be contrasted in the following way :—

3. COMPLEX HETEROZYGOTES

(i) **Introduction.** A "complex heterozygote" is a diploid organism which produces two types of gametes differing profoundly in genetic properties and incapable of giving homozygous offspring. It breeds true primarily by virtue of the elimination of the homozygous embryos.

The determination of these properties by Renner depended on the genetic analysis of a group of *Œnothera* species. The notion of the complex heterozygote, however, is important not only in relation to the special genetic properties of these species and of other species and hybrids which are now being found to resemble them, but also in relation to their analogy with other permanent hybrids —sex heterozygotes and allopolyploids—and to the general problems of variation and hybridity.

Inheritance and chromosome behaviour are so complex in *Œnothera* that, in order to show their relationship to the normal phenomena seen in other organisms, they must be considered together.

(ii) **Inheritance in Œnothera.** The group of *Œnothera* species of the *Onagra* section, which is widely distributed, especially on the eastern side of North America, consists chiefly of forms showing a group of exceptional hereditary properties, as follows :—

1. They breed true in the main when self-fertilised, but throw a certain proportion (1 to 2 per cent. as a rule) of divergent forms (" mutants "). This was first observed by De Vries, who has studied the problem on a very large scale and with great minuteness since 1887. Most of the so-called " mutant " forms have since been found to be trisomic or tetraploid (*cf.* Ch. III), and only differ from the same kinds of mutants in other species in the high frequency with which they appear. Others, however, are diploid, and do not revert to the parental form in later generations.

2. They have a variable proportion (usually 30 to 60 per cent.) of bad seeds in which the embryo has developed little or not at all (Renner, 1916, 1929).

3. When crossed together they usually produce more than one type of hybrid, and reciprocal crosses may be of different types of " twin hybrids," or the same types in different proportions.

4. Some of the diploid mutants (*e.g.*, *Œ. rubrinervis* from *Œ. Lamarckiana*, De Vries, 1918) and crosses (*e.g.*, *Œ. grandiflora* × *Œ. Hookeri*, Cleland and Oehlkers, 1929) yield on self-fertilisation a much higher proportion of new forms than their parents did ; others resemble their parents in hereditary properties, and others again resemble the Californian species, *Œ. Hookeri*, in being absolutely true-breeding and fertile : they have none of their parents' exceptional properties.

The special system of inheritance found in *Œnothera* can be expressed and understood in mendelian terms if we accept the complex-heterozygote hypothesis of Renner (1917, 1924) and the balanced-lethal hypothesis of Muller (1918). The first assumes that each of the mutating species of *Œnothera* is a hybrid that produces two kinds of gametes. These gametes have genetic *complexes* which are distinguished by differences more profound that those that are inherited in a mendelian way in other organisms. They affect the whole habit and structure of the plant, and in this they resemble the sex difference in animals, which also behaves as a unit in inheritance.

The second hypothesis assumes that gametes of neither complex can yield viable homozygotes. Each complex is " lethal " in combination with an identical complex. In terms of Muller's observations on *Drosophila* (1917, 1918), it may be said that each complex of factors is linked with a lethal factor with no crossing-over between them, so that the whole system can be described as a " balanced lethal " mechanism.

A third assumption can then be made, that dissociation through crossing-over occasionally takes place (*a*) between a complex and its lethal factors, and (*b*) between two parts of a complex. The first of these changes will permit the segregation of complete homozygotes ; the second will result in the segregation of plants homozygous for part of the complex. The segregates will be mutants.

Further observations of Renner's (1919, *a* and *b*, 1921) explains differences in the behaviour of different species. He found that the two kinds of pollen grains could often be distinguished by their size and the shape of their starch grains. Often one kind was entirely " inactive," or, owing to its smallness, relatively feeble in growth. Again, in some species he found that, instead of the megaspore at the top (chalazal) end of the row of four, formed in maturation, always giving the functional embryo-sac as it does in *Œ. Hookeri*, the megaspore at the other end often pushed its way round the upper three and usurped the position of the chalazal megaspore. This phenomenon is known as the " Renner effect." Now, if the first division of the mother-cell is the reduction division which separates the two complexes, it will be seen that this competition between top and bottom cells is in reality a struggle for predominance between the two complexes. Where half the embryo-sacs are formed from the micropylar cell and half from the chalazal cell it is natural to suppose that they are all of one complex type which has passed equally often to the top and bottom pole at the first division. The genetic results agree with these conclusions. *Œ. muricata*, which has half its pollen inactive and half its potential embryo-sacs overridden in competition, produces pollen of only one kind, with the *curvans* complex, and embryo-sacs almost all of the other kind, with the *rigens* complex. Such a species as this can therefore breed true and with scarcely any loss of fertility, although it must be heterozygous in the same degree as many interspecific hybrids, because when it is crossed reciprocally with a homozygous species such as *Œ. Hookeri* reciprocal hybrids differ owing to one being a *curvans* hybrid the other a *rigens* hybrid.

This property of "heterogamy" is, however, found in some species which show little evidence of competition. It has therefore been suggested (Rudloff, 1930, 1931) that in these a particular complex passes usually to one end of the embryo-sac, owing to a condition of polarisation analogous to that in the *Caninæ* roses (Ch. XIII). But this is a doubtful analogy, for no sharp difference between chromosomes of opposite complexes has been observed or can be surmised. It is possible alternatively that the elimination of one complex is attained in some species by simple degeneration without competition.

The assumption of the Renner complex, therefore, enables us to describe the phenomena of inheritance and variation in *Œnothera* in mendelian terms, and as an empirical description it is unassailable. But now its material basis has been shown by the study of the behaviour of the chromosomes in the hybrid species and this shows its relationship with other systems.

(iii) **Chromosome Behaviour in Œnothera.** Early observers (Gates, 1908; Geerts, 1908; Davis, 1910) showed that the chromosomes did not always associate simply in pairs in these species but were often attached in chains at diakinesis and metaphase of the first division. It was the work of Cleland, however (1922 *et sqq.*), that first showed this association to have certain constant characters in each species. He found the 14 chromosomes in a diploid *Œnothera* were always associated at diakinesis and metaphase end-to-end in rings of two, four, six or other even numbers, up to fourteen. The size and number of the rings constant for each species, except that occasionally a chain or two chains might replace a ring; just as with the simple pairs which usually form rings, a rod is formed owing to the failure of one of the two chiasmata, in *Œnothera*, as in other organisms with median spindle attachments and complete terminalisation.

The same constancy is found in all hybrids and mutants, and Tables 59 and 60 show some of the results that have been obtained (Cleland, 1928; Cleland and Oehlkers, 1929; Cleland and Blakeslee, 1930; for fuller list, *v.* D., 1931 *d*).

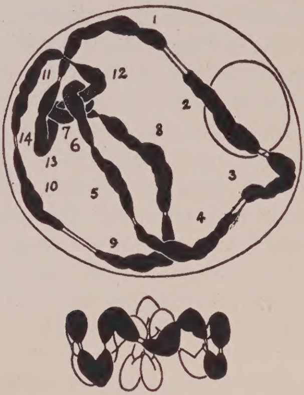


FIG. 101.—First meiotic division in *Œnothera muricata* with a ring of fourteen chromosomes. Above, at diakinesis (showing the self-interlocking of the ring, *cf*. Ch. X). Below, at first metaphase (showing a disjunctional arrangement which gives regular segregation of the two complexes). × 4000. (From D., 1931 *c*. *Cf*. Plate IV.)

Cleland found that the ring of chromosomes usually arranges itself so that successive chromosomes go to opposite poles (Fig. 101). He assumed that the chromosomes had a fixed position in the ring, so that in a ring of fourteen, each of the seven chromosomes of one parental gamete paired at opposite ends with ends of two chromosomes from the other gamete. In this way segregation would only yield two types of gamete, and these two types would be the same as those that had gone to make up the parent zygote. He also assumed that the type of configuration was a specific property of the two complexes of each species or hybrid *in relation to one another*.

This conclusion has been borne out by the extensive observations of recent years. All the complex heterozygote species have multiple chromosome rings. The homozygous forms, whether species or segregates, have seven pairs, or occasionally five pairs and a ring of four.

These observations showed the mechanism by which the segregation of complexes takes place. They showed the consequence of the chromosomes associating in rings, but they did not at once reveal how the complexes came into existence.

In examining this problem Gates, Cleland and Håkansson applied the current theory of chromosome pairing in *Œnothera*. They held that the association of chromosomes at metaphase was derived in all cases from a " continuous spireme " at prophase, in which the chromosomes were associated end to end, unions between homologous and non-homologous chromosomes alternating. The appearance of pairs, on this view, was due to the " segmentation " of the " spireme." It was not seen at that time that the statement that non-homologous chromosomes were associated at metaphase involved a contradiction in terms, for there is no criterion of the homology of chromosomes save their property of pairing at meiosis (Ch. XI, *cf.* D., 1931 *c*).

This theory treated the chromosomes as units, a view that had long been rendered untenable by the observations discussed earlier (Ch. XI). These showed, first, that the pairing properties of the chromosomes were not specific to the chromosomes as wholes but to their constituent parts, and, secondly, that these constituent parts might change places. When it was found that in pairing at prophase in triploids and tetraploids each particle of each of the normal, unaltered, chromosomes had the capacity of independent and specific association it became obvious that ring-formation could be explained in all organisms as the result of pairing, and the formation and terminalisation of chiasmata between exchanged homologous parts of otherwise non-homologous chromosomes

(D., 1929, *a* and *c*). Applying this view to *Œnothera* it was possible to suppose that association took place at meiosis only between homologous parts of chromosomes. Since the chromosomes are only associated at their ends it is only necessary, in considering their pairing properties, to regard them as made up of two "segments" which are effective in pairing. In this way a homozygous *Œnothera* with seven pairs of chromosomes at meiosis would have a constitution as follows (homologous segments bearing the same letters):

7(2) (*AB* (*CD* (*EF* (*GH* (*KL* (*MN* (*OP*
AB) *CD*) *EF*) *GH*) *KL*) *MN*) *OP*)

while a complex heterozygote with a ring of 14 chromosomes would be made up as follows:

(14) (*AB* *CD* *EF* *GH* *KL* *MN* *OP*
╲ ╱ ╲ ╱ ╲ ╱ ╲ ╱ ╲ ╱ ╲ ╱ ╲
BC *DE* *FG* *HK* *LM* *NO* *PA*)

It was supposed that this arrangement of segments arose as a result of successive interchange in the ancestry of the plant, as had been inferred in simpler cases in *Datura* (Blakeslee, 1928). Thus an ancestor with simple pairs, such as that given, would by interchange between *B* and *D* give new chromosomes *BC* and *DA*, which would form a ring of four with the parental type, as follows:

(4) + 5(2) (*AB* *CD* (*EF* (*GH* (*KL* (*MN* (*OP*
╲ ╱ ╲
BC *DA*) *EF*) *GH*) *KL*) *MN*) *OP*)

This hypothesis explains the constancy of the behaviour of the species, both in heredity and in chromosome association, for each of the complexes is made up in a specific and constant arrangement. The dissimilarity of the complexes is correlated with the dissimilarity in the arrangement of the segments in the two kinds of gametes produced by each species. Just as each plant is the result of the fusion of two complexes, so also is it the result of the fusion of gametes differing in respect of the arrangement of segments in such a way as to give the chromosome ring characteristic of the species. It is a hybrid in respect of the arrangement or *structure* of its chromosomes (Ch. V).

The hypothesis also explains their behaviour on hybridisation, for Cleland and Blakeslee (1930) have been able to predict from the configurations seen in crosses of two species with a third what configurations would be found in a cross between the first two. These predictions were verified.

(iv) **Mutations.** Finally, the hypothesis explains the origin of the diploid mutations. Most of these have changed chromosome configurations as the result of further segmental interchange. Interchange has occurred in the species' ancestors, and it is assumed that it will go on occurring in the species themselves, although no further increase in the size of the ring is possible. Two kinds of interchange are probably most important (D., 1931 *d*): first, interchange between chromosomes of opposite complexes and, secondly, interchange between chromosomes of the same complex.

As an example of the first we can consider the so-called "half-mutants" of *Œ. Lamarckiana*. This species is a heterozygote made up of two complexes, *velans* and *gaudens*. It has a ring of twelve and one pair at meiosis. Take its composition to be as follows:

$$\begin{array}{llllllllllllll}
\textit{velans} & (A_vB & & C_vD & & E_vF & & G_vH & & K_vL & & M_vN & & (OP \\
 & & \diagdown\ \diagup & & \diagdown\ \diagup & & \diagdown\ \diagup & & \diagdown\ \diagup & & \diagdown\ \diagup & & \diagdown & \\
\textit{gaudens} & & B_gC & & D_gE & & F_gG & & H_gK & & L_gM & & N_gA) & OP)
\end{array}$$

(Each chromosome is given the initial letter of its complex to distinguish it. This is put in the middle for a reason that will be seen later.)

The exchange of segment A of A_vB with segment G of F_gG will give two new chromosome types G_vB and F_gA, and a new kind of segregation giving a gamete containing all the necessary 14 segments arranged as follows:

subvelans $B_gC, D_gE, F_gA, G_vH, K_vL, M_vN, OP.$

This will unite with an unchanged *velans* gamete to give a ring of six and four pairs, as follows:

$$\begin{array}{lllllllllll}
\textit{velans} & (A_vB & & C_vD & & E_vF & & (G_vH & (K_vL & (M_vN & (OP \\
 & & \diagdown\ \diagup & & \diagdown\ \diagup & & \diagdown & & & & \\
\textit{subvelans} & & B_gC & & D_gE & & F_gA) & G_vH) & K_vL) & M_vN) & OP)
\end{array}$$

Such is the configuration found in the so-called "half-mutant" *rubrinervis*, which appears in the selfed progeny of *Œnothera Lamarckiana* once in a thousand seedlings.

Moreover, it will be seen that the mutant, on this hypothesis should consist of two complexes, one unchanged *velans*, the other a mixture of *velans* and *gaudens*. This is in agreement with the conclusions of the geneticist (*cf.* Hoeppener and Renner, 1929) who describes the two as "*pænevelans*" and "*subvelans*." *Pænevelans* is the *velans* complex derived normally from *Lamarckiana*; the slight difference it shows in later generations from the *velans* of the parental form is probably due to crossing-over in the half-mutant with *subvelans*. This mutant yields one-quarter bad seeds, one-half seedlings like itself with the same chromosome configuration, and one-quarter *subvelans.subvelans*, which is the "full-mutant" *Œ. deserens*. This form, being homozygous, has seven pairs of chromosomes (7(2)) at meiosis. It arises, we may say, because *subvelans* no longer includes the chromosomes with the lethal factors of *velans*.

Segmental interchange between chromosomes of the same complex will have a different result, for the seedlings, whose parental gametes have suffered the change, will not differ in appearance from their parents, but their chromosomes will pair differently. Where the parents had a ring of 14 chromosomes the seedlings will have two rings, (12) + (2) or (10) + (4) or (8) + (6). Now the rule that plants with the multiple ring breed true to this character need not apply equally to the small rings derived from it. *Œ. biennis* ((8) + (6)) breeds true because, presumably, each ring is preserved by its lethal system; but where one ring is broken into two by interchange each half will not necessarily have its lethal system. A new ring of four chromosomes in a plant from two gametes, one of them with chromosomes *AB* and *CD* the other with chromosomes *BC* and *DA*, may yield homozygous progeny either of the type *AB–AB*, *CD–CD* or the type *BC–BC*, *DA–DA* if either of these is viable (*i.e.*, has no factors lethal in the homozygous condition). Hence a plant whose parental gametes have undergone interchange between chromosomes of the same complex may be expected to yield progeny homozygous in regard to the members of one of the small derived rings in high proportions by a process which is essentially one of mendelian segregation. Such is a possible explanation of the origin of "mass-mutation" in *Œ. Reynoldsii*

(Kulkarni, 1929 ; Bartlett, 1915 ; D., 1931 *c*), but the chromosome constitution of the mutants has not yet been described.

The cytological and genetical observations seem to be brought into the closest agreement therefore by two assumptions : First, ring-formation in *Œnothera* is determined by the specific pairing properties of the parts of the chromosomes as in other organisms, and therefore segmental interchange has occurred (and is occurring) in these species. Secondly, each particular arrangement of segments in a set of seven chromosomes making up one gamete is associated with the character of a genetic complex.

In order to examine these assumptions, it is necessary first to consider the conditions under which the chromosomes come to associate in rings during the prophase of meiosis in *Œnothera*. Recent evidence (Catcheside, 1931, 1932) shows that they are the same as in other interchange heterozygotes (Ch. V). Segments pair with their homologues so far as they correspond ; where the correspondence ceases they change partners (McClintock in Zea, 1931 ; *cf.* D., 1931 *d*). Chiasmata are formed in the paired segments, and these are terminalised (*cf.* Gairdner and D., 1931), in *Campanula persicifolia*. In polyploid *Œnothera* there are therefore multiple chiasmata, as in *Tradescantia*, *Rosa*, and *Primula*. But a question arises, if chiasmata are formed, and crossing-over therefore occurs between each pair of segments : where are the differences situated which constitute the complexes and between which no crossing-over, and therefore no pairing, occurs ?

Clearly they must lie in the neighbourhood of the spindle attachment, for all association must take place distally to them if they are not first to arrest terminalisation and, secondly, to cross-over to opposite chromosomes (Chs. X and XII, *cf. Enchenopa*, p. 387).

This condition might easily be brought about by translocation of small pieces from one chromosome to the middle of another. These would not continue the homologies of the terminal segments. Moreover, the different (independent) distributions of material in the middle parts of the chromosomes of the two complexes would give a different genetic character to each complex and would prevent its being viable in the homozygous condition. This is the justification for marking each chromosome in the middle with the initial letter of its complex. Finally, such a system would account for the occurrence of occasional segmental interchange by crossing over between homologous segments intercalated in chromosomes that are otherwise non-homologous.

The simplest case of this may be shown diagrammatically and taken to represent the origin of ring-formation in *Œnothera, Campanula, Pisum* and other genera (Fig. 102). Translocation of a segment *x* from a chromosome *AxB* to another chromosome *CD* will give, in the hybrid between the old and new (*AxB, AB, CxD, CD*) by occasional crossing-over in the *x* segments, new chromosomes of the constitution *AxD* and *BxC*. These will form a ring if they meet the opposite type *AB* and *CD*, and we shall have from the new ring-of-four two types of gametes which will differ both in the arrangement of the segments and in the number of *x* segments in the "complex" (a difference in respect of which crossing-over will obviously be impossible).

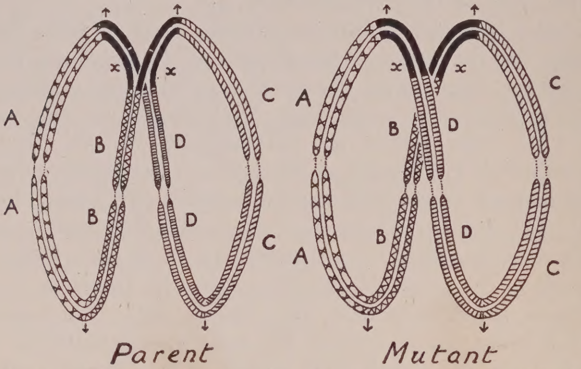


FIG. 102.—Diagram showing the first metaphase (disjunctional) arrangement of two pairs of chromosomes with crossing-over between two homologous intercalary segments (as observed in *Œnothera* and *Pisum*) and the resulting ring-of-four in the progeny. Thus a translocation heterozygote gives an interchange-cum-reduplication heterozygote.

Thus in one step a ring of four will be produced which will breed true, for neither type of gamete will yield a satisfactory homozygote. In one step the Renner complex, the balanced lethal and the ring mechanism will have been established.

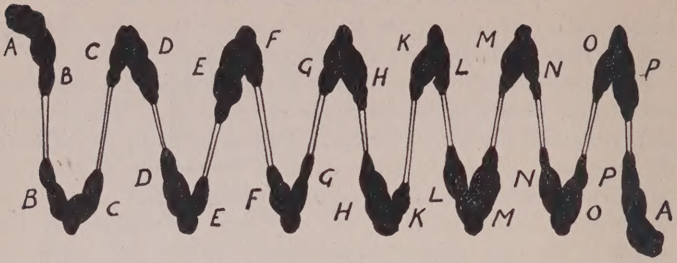
Recent cytological observations on *Œnothera* show that segmental interchange occurs by crossing-over in this way. Ring-forming plants occasionally have chiasmata formed interstitially between chromosomes, which do not associate terminally in the ring (p. 267). These chiasmata remain interstitial and are seen at metaphase. Evidently there are segments intercalated in the middle of the ring-forming chromosomes which do not follow the homologies of the ends (Fig. 103). Crossing-over between them at the chiasmata formed gives new segmental interchange as required by the theory of the origin of half-mutants set out above. The existence of such segments is evidence that the differences between Renner complexes are the product of structural changes, apart from mere interchange, taking place independently in different complexes and giving each complex a characteristic genetic balance, just as such changes in the sex chromosomes are supposed to give the special differential balance to the two sexes.

Their occurrence has recently been shown by the same behaviour in an artificial *Pisum* hybrid with a ring-of-six (E. R. Sansome, 1932). Both observations constitute evidence of crossing-over at a chiasma (Ch. X, Fig. 71 and Plate IV).

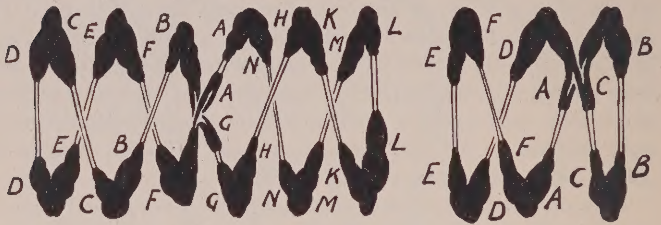
It may equally be supposed that segmental interchange occurs as a direct change through the entanglement of two chromosomes at pachytene (*cf.* Serebrovsky, 1929). A direct change of this kind has been produced by X-raying *Drosophila* (Muller, 1930 *b*), and such has been the method of origin usually assumed. Probably both methods are important in nature.

Interchange will always lead to the production of interchange heterozygotes in the first generation just as gene mutation leads to the production of mendelian heterozygotes. These will segregate homozygous new and old forms in the next generation unless the interchange is associated (as suggested above) with the production of a lethal type. In the latter case a permanent interchange heterozygote will arise directly. In the former case the permanent heterozygote will only appear following hybridisation after an interval during which changes have taken place that are necessary

Chain of Fourteen Chromosomes in Oenothera.

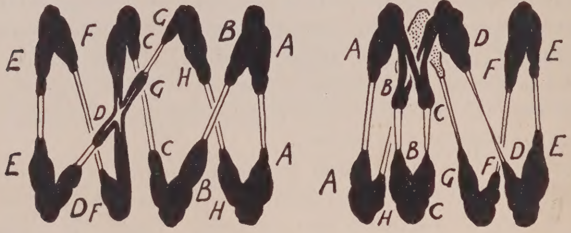

A
B
C
D
E
F
G
H
K
L
M
N
O
P
B
C
D
E
F
G
H
L
K
M
N
P
O
A

The Occurrence of Segmental Interchange between:-


D
C
E
B
F
A
H
K
M
L
N
A
G
E
B
L
H
D
C
F
G
N
K
M
E
F
D
B
A
C
F
E
B
C
D
A

(i) Non-Corresponding Segments of Opposite Complexes (to give half-mutants in Oe. Lamarckiana.)

(ii) Corresponding Segments of the Same Complex (to give mass mutants in Oe. Reynoldsii)


E
F
G
C
B
A
G
H
D
E
C
A
D
F
B
H
A
D
E
F
B
C
B
D
E
A
G
F
H
C

(iii) Corresponding Segments of Opposite Complexes (new combination non-disjunctional.)

(iv) Non-Corresponding Segments of the Same Complex (to give change of pairing type in Oe. pratincola.)

FIG. 103.—Diagram showing normal and anomalous pairing of chromosomes inferred in complex-heterozygote *Œnothera* with rings of various sizes. Segmental interchange of the first two types will yield mutant gametes. The third type will give no viable mutant and the fourth type will give a gamete having the same properties *vis-à-vis* its normal partner but changed properties *vis-à-vis* others. (*Cf.* D., 1931 *d* and Plate IV.)

to make the segregation of homozygotes from the hybrid impossible or difficult.

The steps in this indirect process of origin are shown in *Campanula* (Gairdner and D., 1931) where crosses between structurally different forms give rings of six which yield a high proportion of their like when selfed. Probably both the direct and the indirect method have played some part in the origin of the complex heterozygote species of *Œnothera.*

Diploid mutations not involving segmental interchanges are more simply explained. Genetically they are described as crossing-over in respect of lethal factors, so that one of the two complexes of a heterozygote emerges in a homozygous form. In this way the mutant *ochracea*, 7 (2), appears spontaneously from *Œ. grandiflora*, (14), (De Vries, 1918), and the mutant *lutescens* after hybridisation from *Œ. suaveolens* (Renner, 1927). Both can be understood as a result of exceptional crossing-over in the middle parts of the chromosomes, so that lethal combinations are replaced by non-lethal. This occurs in *Œ. grandiflora* normally ; in *Œ. suaveolens* only when the *flavens* complex is associated with a different complex in the hybrid with *Œ. biennis*. Such a difference in behaviour depending on a difference in partner is to be expected if crossing-over is the basis of these mutations, for crossing-over is conditioned by the presence of a partner for the region in which it occurs : it is a relational phenomenon.

The mutations involving changes in chromosome number are to be explained as the result of irregularities in chromosome distribution at meiosis, such as those occurring in other organisms. The fact that they occur in much greater numbers than in other species is due to the mechanical conditions of separation in a ring. Normally a ring segregates " disjunctionally," *i.e.*, so that the chromosomes that are paired pass to opposite poles. This orientation can be supposed to be due to the force of repulsion between attachment constrictions being an inverse function of distance and being most effective axially in the spindle (*cf.* Ch. XII), so that adjoining chromosomes repel one another more effectively than distant ones. It will be seen that if this orientation takes place almost simultaneously in different parts of the ring, sometimes chromosomes separated by an even number will come to lie to one side of the equator and two of the intervening chromosomes must then pass to the same pole, or one be left on the equator to divide equationally at the first division. These occurrences have been observed both in *Œnothera* (Cleland, 1925 *et al.*; D., 1931 *d*) and in *Rhœo* (D., 1929 *c*) where a ring of 12 chromosomes is formed and conditions of segregation can be more easily studied than in *Œnothera.* Irregularities must necessarily occur in the intervening chromosomes in *both* directions round the ring, so that non-disjunction is always double. If the ring is replaced by a chain the non-disjunctional result occurs, although the two chromosomes which pass to the same pole may not have been joined, but only have been capable of having been joined. Where the non-disjunctions occur on the same side of the equator two gametes with eight and six chromosomes are formed instead of seven and seven. The high frequency of this occurrence is responsible for the high frequency of trisomics (1·5 per cent. in *Œ. Lamarckiana*). The lagging of chromosomes of undecided orientation is probably responsible for the failure of separation of two daughter-nuclei and the formation of unreduced gametes (Schwemmle, 1927; D., 1931 *d*). From these occasional tetraploid and triploid seedlings arise, the *gigas* and *semi-gigas* mutants of De Vries.

The general bearing of these observations will be considered in relation to the evolutionary problem (Ch. XVI).

TABLE 59

Summary of Ring-forming Properties in Forms of *Œnothera*

1. SPECIES.

Species	Complex constitution	Configuration
Heterozygotes :—		
Œ. grandiflora	acuens.truncans	(14)
Cockerelli	curtans.elongans	(14)
strigosa	deprimens.stringens	(14)
muricata	curvans.rigens	(14)
suaveolens	flavens.albicans	(12) + (2)
Lamarckiana	velans.gaudens	(12) + (2)
biennis	rubens.albicans	(8) + (6)

Hybrid.	Complex constitution.	Configuration.
Homozygotes :[2]		
franciscana	^{h}franciscana.^{h}franciscana	(4) + 5 (2)* or 7 (2)
Œ. Hookeri	^{h}Hookeri.^{h}Hookeri	7 (2)
purpurata	^{h}purpurata.^{h}purpurata	7 (2)
2. HYBRIDS BETWEEN HETEROZYGOTES.		
Heterozygotes :[2]		
Œ. grandiflora × *Lamarckiana.* (and reciprocally)	(i) acuens.velans	(6) + (4) + 2 (2)
	(ii) acuens.gaudens	(14)
	(iii) truncans.velans	(10) + (4)
	(iv) truncans.gaudens	(10) + (4)
Œ. Lamarckiana × *strigosa.* (and reciprocally)	(i) velans.stringens	(6) + (4) + 2 (2)
	(ii) gaudens.stringens	(14)
	(iii) deprimens.velans	(10) + 2 (2)
	(iv) deprimens.gaudens	(10) + 2 (2)
Œ. Lamarckiana × *suaveolens.* (and reciprocally)	(i) velans.flavens	2 (4) + 3 (2)
	(ii) gaudens.flavens	(12) + (2)
	(iii) albicans.velans	(14)
	(iv) albicans.gaudens	(8) + (6)
Œ. suaveolens × *strigosa.*	(i) flavens.stringens	(4) + 5 (2)
	(ii) albicans.stringens	(12) + (2)
	(iii) deprimens.flavens	(12) + (2)
	(iv) albicans.deprimens	(not obtained)
Homozygotes :[2]		
Œ. suaveolens × *strigosa.*	flavens.stringens	7 (2)†
3. HYBRIDS BETWEEN HOMOZYGOTES AND HETEROZYGOTES.		
Homozygote :		
Œ. Lamarckiana × *grandiflora.*	truncans.velans	7 (2)†

* The two complexes are not genetically distinguishable.

† The two complexes are not structurally distinguishable, and are very similar genetically.

4. HYBRIDS BETWEEN HOMOZYGOTES (Gates and Catcheside, 1931).

Hybrid	Complex constitution	Configuration
Heterozygotes :[2]		
Œ. deserens × *blandina*	—	(6) + 4 (2)
Œ. deserens × *purpurata*	—	(4) + 5 (2)
Œ. blandina × *purpurata*	—	(4) + 5 (2)

5. DERIVATIVES OF HYBRIDS.

Hybrid	Complex constitution	Configuration
Œ. lutescens (ex *suaveolens* × *biennis*).	$^{\text{let.}}$flavens.^{x}flavens	7 (2)*
Œ. suaveolens × *pachycarpa.*	—	F_1 and F_2 (6)+(4)+2 (2) F_2 (6) + 4 (2)

6. MUTANTS.

Hybrid	Complex constitution	Configuration
Œ. rubrinervis (ex *Lamarckiana*).	subvelans.pænevelans	(6) + 4 (2)
Œ. ochracea (ex *grandiflora*).	acuens.acuens	7 (2)

7. DERIVATIVES OF MUTANTS.

Hybrid	Complex constitution	Configuration
Œ. deserens (ex *rubrinervis*).	subvelans.subvelans	7 (2)

* The two complexes are not structurally distinguishable, and are very similar genetically.

TABLE 60

The Numbers of Species, Hybrids and Mutants in *Œnothera* having Different Types of Configuration compared with their Frequency if Segments were assorted at Random (after Haldane, in D., 1931 *d*).

Configuration type.	Relative random frequency (Total Possibilities, ×135,135).	Observed Frequency.				
		Species.	"Mutants" or segregates of species.	"Hybrids."	Derivatives or segregates of hybrids.	Totals.
1. (14)	23,040	12	—	15	—	27
2. (12) + (2)	13,040	5	—	16	—	21
3. (10) + (4)	8,064	—	—	5	—	5
4. (8) + (6)	6,720	2	—	2	—	4
5. (8) + (4) + (2)	5,040	—	—	1	—	1
6. (10) + 2(2)	4,032	—	—	11	—	11
7. 2(6) + (2)	2,240	—	—	—	—	0
8. (6) + 2(4)	1,680	—	—	1	—	1
9. (6) + (4) + 2(2)	1,680	—	—	3	1	4
10. (8) + 3(2)	840	—	4	1	1	6
11. 3(4) + (2)	420	—	—	—	—	0
12. 2(4) + 3(2)	210	—	—	3	—	3
13. (6) + 4(2)	140	—	3	5	2	10
14. (4) + 5(2)	21	1	1	8	—	10
15. 7(2)	1	4	6	3	4	17
Totals	67,568	24	14	74	8	120

CHAPTER XV

APOMIXIS

Classification—Apomixis and the Life Cycle—Parthenogenesis—The Haplo-Diploid System—Apogamy—Apospory—Adventitious Apomixis—Meiosis in Functional Cells—In Non-Functional Cells—Pseudogamy—Conditions Determining Apomixis—Chromosome Numbers of Apomictic Plants.

1. DEFINITION AND CLASSIFICATION *

APOMIXIS may be defined (following Winkler, 1908) as a system of reproduction having the external character of sexual reproduction but omitting one or both of its essential internal processes. These are meiosis and fertilisation. Clearly if only one of these is omitted the irregularity cannot become a habit, and examples of such non-recurrent abnormalities will be specially considered. The abnormality is recurrent where both processes are omitted from the life cycle, and this happens in species of all the principal groups except the Vertebrata, Echinoderma, Bryophyta and Gymnospermæ (*cf.* Ernst, 1918; Winkler, 1920).

Where the specialised reproductive cells, spore and egg-cell, continue to function the abnormality is known as *parthenogenesis*. An important distinction can then be made between a type of parthenogenesis in which fertilisation fails first, and a type in which meiosis fails first. The effect will be that, in the first, both generations (normally haploid and diploid) will be haploid, when the reproduction is called *haploid parthenogenesis*, and in the second, both generations will be diploid, when the reproduction is called *diploid parthenogenesis* (Fig. 104). It will be seen that this distinction can only be made with certainty where the origin of the new system is known or the normal type of reproduction can be compared with the aberrant; this, however, is usually possible. Further, in such a case as that of apparent diploid parthenogenesis in *Chara crinita*

---

* The usage of terms in this chapter is that found most convenient in approaching the matter from a genetic point of view. Confusion in the terminology is due to writers approaching it from different points of view.

(Ernst, 1918) it is possible, although not plausible, to assume that failure of a mitotic division, not failure of meiosis, was the starting-point of a parthenogenetic mode of reproduction (*cf.* Winkler, 1920).

In the higher animals the specialised germ-cell is always the immediate product of meiosis or some modification of meiosis in the specialised mother-cell, and where meiosis fails in parthenogenesis the specialised function of the mother-cell (oöcyte) and the gamete (egg-cell) are always retained. But in plants with an alternation of generations there are specialised spore mother-cells and specialised gametes developed at different parts of the life cycle, and unspecialised cells may be substituted for either or both of these when meiosis and fertilisation are omitted. Thus not only the characteristic processes but also the characteristic organs of sexuality are lost. Where the spore mother-cell either fails to develop or does not function in reproduction we speak of *apospory*, and where the normal gamete cell does not function we speak of *apogamy*. When both of these are combined only the external character of seed production distinguishes the development of the embryo from vegetative propagation.

Apomixis will first be considered in relation to the life cycle in the most important groups in which it occurs.

2. APOMIXIS IN RELATION TO THE LIFE CYCLE

(i) **Higher Animals (Metazoa).** (*a*) DIPLOID PARTHENOGENESIS. In many species of insects, crustaceans and nematodes this form of parthenogenesis is obligatory. Parthenogenetic females produce only their like, by a failure of meiosis at maturation in the oöcyte. In others, parthenogenesis is facultative: parthenogenetic females may give rise to sexual females and sexual males. In some of these (*e.g.*, *Daphnia*, Banta *et alii*, 1926, and Rotifera) the succession of sexuality and parthenogenesis is irregular, in others they come in a definite cycle (*e.g.*, in Aphides). The conditions immediately determining this cycle will be seen later.

(*b*) HAPLOID PARTHENOGENESIS. In several groups of Metazoa sexual females give female offspring when their eggs are fertilised, male when they are not fertilised, as first shown in the bee by Dzierzon. This is believed to be the method of sex differentiation in the Hymenoptera, Rotifera, and in some Thysanoptera, A and Hemiptera. In the Rotifera, generations of females reproc by diploid parthenogenesis can be intercalated between the s generations, as in the Aphides. In the hymenopteran *Neur* certain females lay only fertilised eggs and others only unferti

It has been shown in several of these groups that the femal in fact, diploid and the males haploid. The sex differentiatio not depend, therefore, on any segregation (and resulting differ balance), but on a purely quantitative difference. The eviden this method of sexual differentiation, especially in Thysanopte Rotifera, is chiefly from breeding results. But in the foll instances the assumption of male haploidy has been fully v cytologically (*cf.* Schrader and Hughes-Schrader, 1931).

TABLE 61

Examples of Haplo-Diploid Sex Differentiation

Acarina	*Tetranychus bimaculatus*	$n = 3$	Schrader, 1923.
Hemiptera (Aleurodidæ)	*Aleurodes proletella*	$n = 13$	Thomsen, 1927.
	Trialeurodes vaporariorum	$n = 11$	Hughes-Schrader,
(Coccidæ)	*Echinicerya anomala* *Icerya* spp.	$n = 4$	,, ,,
	Icerya purchasi (☿ and ♂)		,,
Hymenoptera	*Apis mellifica*	$n = 16$	Nachtsheim, 1913
	Paracopidosomopsis floridanus.	$n = 8$	Patterson and H 1925.
	Pteronidea ribesii	$n = 8$	Peacock and San 1931.
	(also probably in *Vespa*, *Neuroterus*, *Habrobracon* an genera).		
Rotifera	*Asplanchna* spp.		Whitney, 1928.

The mode of reproduction in *Icerya purchasi* is exception particularly significant. Fertilised eggs give hermaphrodites. produce 1 per cent. of eggs that go unfertilised, and give h males and 99 per cent. that are fertilised either by the sperm hermaphrodite or by that of the males. The species therefo an alternative system of reproduction between hermaphroditis haplo-diploid sex differentiation (Fig. 108).

Icerya purchasi also has a unique peculiarity in the de ment of the testes in the hermaphrodite. The haploid num

›mosomes is found in the spermatogonia, presumably through e process analogous to meiosis having occurred during their elopment. The testes are, therefore, genetically male and the ›rmaphrodite " diploid, genetically female, since it only produces ›m in tissue developed by a special abnormality and genetically : of a different individual. The genetic differentiation of loid and diploid is therefore as sharp as that in the Hymenoptera the system of reproduction in *Icerya* is probably derived from simple haplo-diploid type (Ch. XVI).

i) **Ferns (Pteridophyta).** In the ferns the two generations have ndependent existence, and it is therefore possible to distinguish different abnormal sexual processes more readily than in the ›ering plants. Nevertheless a great deal of the older work in field is, as Manton (1932) says, ambiguous. All types naturally ırring involve the suppression of meiosis and fertilisation and › be classified as follows :—

ı) DIPLOID PARTHENOGENESIS, *i.e.*, without loss or substitution ıe special organs—spores and gametes (*e.g.*, *Marsilia Drummondii*, ısburger, 1907). In this type two diploid spores are formed as sult of the failure of reduction, instead of four haploid ones, and egg-cells developed on the diploid prothallia (gametophytes) › into sporophytes without requiring fertilisation.

) APOSPORY, *i.e.*, with substitution of unspecialised cells for the ›es (*e.g.*, *Athyrium Filix fœmina* var. *clarissima* Bolton, and *opendrium vulgare* var. *crispum Drummondæ*, Farmer and by, 1907). In this type the gametophyte does not develop from ›ore but as a purely vegetative outgrowth of the sporangium or tip of the frond. It is diploid, meiosis having been completely tted, and it produces diploid egg-cells which develop without ilisation (*cf.* Andersson-Kottö, 1931).

) APOGAMY, *i.e.*, with substitution of unspecialised cells for the ıetes (*Nephrodium hirtipes*, Steil, 1919). In this type the ›ophyte arises as a purely vegetative outgrowth from the ıetophyte (prothallium), which is diploid, having arisen from ›duced spores. In the example, antheridia were produced ough there were no archegonia. The failure of reduction was ently due, as in *Marsilia*, to the formation of restitution nuclei following imperfect pairing of the chromosomes at the first meiotic division (*cf.* Rosenberg, 1927, 1930).

(*d*) Apospory with apogamy (*Athyrium Filix fœmina* var. *clarissima* Jones, Farmer and Digby, 1907 ; *Nephrodium pseudo-mas,* Rich. var. *cristata,* Digby, 1905). In this type both the alternating generations arise from unspecialised cells by purely vegetative processes.

These abnormalities may be variously combined with one another in the same individual (Digby, 1905).

(iii) **Flowering Plants (Angiospermae).** In the angiosperms the same types of abnormality occur as in the ferns. Relatively few of the great number of forms which are known to be apomictic from genetic experiment have yet been studied cytologically.

The following classification applies to the ways in which an embryo may develop asexually in the angiosperms ; it is not a final classification of the habits of species, for it is often found that when sexuality fails it is replaced in several competing ways in the same species.

(*a*) Diploid Parthenogenesis. Three types of diploid parthenogenesis are recognised (*cf.* Rosenberg, 1930 : *v.* Fig. 104).

1. *Antennaria* type (Juel, 1900). The mother-cell develops " directly " into the embryo-sac.

Elatostema sessile, Strasburger, 1910.
Erigeron annuus, Holmgren, 1919.
Eu-Hieracium spp., Rosenberg, 1917, 1927.
Ochna serrulata, Chiarugi and Francini, 1930. (*Cf.* Francini, 1928).

2. *Taraxacum* type (Juel, 1905). The mother-cell divides once and the lower cell develops directly into the embryo-sac.

Chondrilla juncea, Rosenberg, 1912.
Taraxacum albidum, Osawa, 1913.
Balanophora japonica, Kuwada, 1928.

3. *Alchemilla* type (Murbeck, 1901). The mother-cell divides twice and one of the four daughter-cells develops into the embryo-sac.

Thismia javanica (probably), Meyer, 1925.
Artemisia nitida, Chiarugi, 1926.

In normal reproduction the female gametophyte (the embryo-sac) may be derived from one, two, or all four of the spores produced by meiosis in the mother-cell. It is therefore impossible, in parthenogenetic plants which would normally be of the last type, to tell whether a second division of the embryo-sac mother-cell is essentially a part of meiosis, or the first somatic division of the gametophyte. The three types that are found in parthenogenetic angiosperms do not therefore correspond directly with the three types in their sexually reproducing relatives. The suppression of meiosis must be supposed to follow similar lines to that most frequently followed in the pollen mother-cells, *viz.*, the production of two cells instead of four by the dividing mother-cell. In the *Antennaria* type, therefore, we must regard the first of the divisions of the embryo-sac as homologous with the abortive meiosis, and in the *Alchemilla* type we must suppose that the chromosomes divide equationally at each division as elsewhere.

In *Artemisia nitida* a multinucleate archesporium (*i.e.*, a group of several mother-cells) has been found to give rise to both reduced and unreduced embryo-sacs in the same ovule. The unreduced ones can develop parthenogenetically. In *Ochna serrulata*, on the other hand, there is sometimes no clear differentiation of archesporial tissue, so that the distinction between apospory and parthenogenesis fades away.

The behaviour of the polar nuclei is variable in parthenogenesis. Clearly the same three to two proportion in the nuclear content of endosperm and embryo cannot usually be established as in sexual reproduction. It has been found that in *Erigeron annuus* (Holmgren, 1919) the polar nuclei fuse, while in *Balanophora* (Ernst, 1913) they do not. *Zephyranthes* is remarkable in one generative nucleus of the pollen fusing with a polar fusion-nucleus, so that the endosperm is sexually produced, while the other generative nucleus does not fuse with the egg cell (Pace, 1913).

(*b*) Apogamy, the development of other cells than the egg cell into the embryo sporophyte, is probably not very important. The synergids and antipodal nuclei have been supposed to give rise to supernumerary embryos in the facultatively parthenogenetic *Allium odorum* (Haberlandt, 1923). In order to give diploid embryos they must first fuse in pairs or fail to separate at mitosis. Such a doubling in the antipodal nuclei is characteristic of a section of the related genus *Tulipa* (Ch. III).

(*c*) Apospory, the development of other cells than the embryo-sac cell into the gametophyte, is probably important in many species. In *Hieracium Pilosella* cells in the nucellus or integument may develop into embryo-sacs, which, of course, are diploid (Rosenberg, 1906, 1930). These compete successfully with the reduced embryo-sac in development and usurp its function. This is reminiscent of

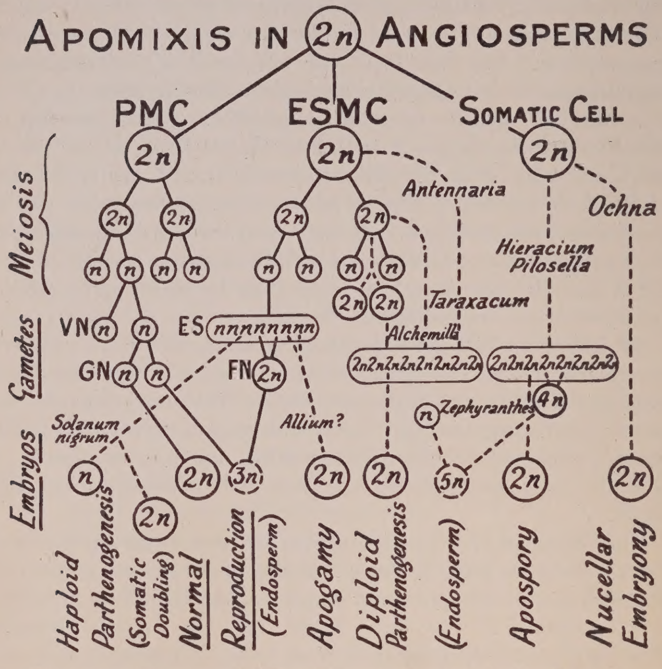

APOMIXIS IN 2n ANGIOSPERMS
PMC
ESMC
SOMATIC CELL
Meiosis
Gametes
Embryos
2n
2n 2n
n n n n
VN n
n
GN n n
ES nnnnnnnn
FN 2n
2n 2n
n n n n
2n 2n
2n
Antennaria
Ochna
Hieracium Pilosella
Taraxacum
Alchemilla
2n2n2n2n2n2n2n2n
2n2n2n2n2n2n2n2n
4n
n
Zephyranthes
Solanum nigrum
Allium?
n
2n
2n
3n
2n
2n
5n
2n
2n
Haploid Parthenogenesis
(Somatic Doubling)
Normal Reproduction
(Endosperm)
Apogamy
Diploid Parthenogenesis
(Endosperm)
Apospory
Nucellar Embryony

Fig. 104.—Diagram of different forms of apomixis found in the flowering plants. Unbroken lines show the course of sexual reproduction, broken lines, of apomixis. The species given are not all fixed in the particular kind of apomixis here assigned to them (*cf.* Table 63).

the Renner effect (Ch. XIV). Apospory is also found in *Artemisia nitida* (Chiarugi, 1926) and in *Ochna serrulata* (Chiarugi and Francini, 1930).

In all these species the normal embryo-sac has a chance of developing, either by fertilisation, as in *Hieracium*, or parthenogenetically, as in *Artemisia* and *Ochna*. The first is conditioned by the formation of a viable gamete in a plant which is slightly sterile sexually owing to hybridity ; the second is conditioned by the formation of a diploid embryo-sac cell by the successful suppression of meiosis in a plant in which this suppression has not become a constant process. Apospory may then be said to be characteristically developed in those plants which are too hybrid to be regularly sexual or not hybrid enough to be regularly parthenogenetic. It bridges the gap.

(*d*) APOSPORY WITH APOGAMY occurs in two ways. *Nucellar Embryony* is the purely vegetative development of cells in the nucellus or integument into the embryo sporophyte. It gives supernumerary embryos in sexually reproducing plants (*e.g.*, *Citrus*, *Zygopetalum*), and occurs as with parthenogenesis in *Alchemilla*, *Nothoscordon fragrans*, and *Ochna* " *multiflora*," which are sexually sterile.

Vivipary is the replacement of the flower by a purely vegetative outgrowth, which is capable of propagating the plant as a bulbil. It is principally developed facultatively and then shows considerable variation subject to environmental influence. It is found especially in *Allium*, *Poa*, and *Festuca*. The imposture is recognisable at once from the external morphology of the organism, so that this method of reproduction need not be described as apomixis.

For simplicity the different abnormalities of reproduction have so far been considered separately, but in their occurrence they are not easily separable. It is common for apomictically reproducing plants to show several abnormalities together. This is particularly well exemplified by *Artemisia nitida* (Chiarugi, 1926). This triploid species is sexually sterile and its normally produced megaspores die, their place being taken by aposporous embryo-sacs. Failure of reduction gives diploid parthenogenesis of all three types so that seed may develop in four ways (Table 63).

Which of these different types of reproduction can be successful is probably decided by competition. Clearly the haploid or irregularly reduced embryo-sac of a hybrid will stand little chance against the somatic embryos. Where numerical reduction has failed the odds will be reversed. This competition has been well illustrated by Haberlandt (1921 *b*) in *Hieracium flagellare*. Such competition is perhaps characteristic of all stages of development of gametophytes and embryos in hybrids, as in *Œnothera* (Ch. XIV).

A different range of abnormality is found in *Allium odorum* according to Modilewski (1930). The egg-cell develops in one of four ways : (i) normally, after reduction and double fertilisation ; (ii) after failure of reduction with fertilisation of the fusion nucleus, so that the embryo is diploid, the endosperm pentaploid, as in *Zephyranthes* ; (iii) after failure of reduction but without fertilisation of the fusion nucleus ; (iv) by haploid parthenogenesis. The last two processes result in degeneration at an early stage : fertilisation, single or double, is indispensable.

(iv) Lower Organisms (Thallophyta and Protista). Amongst the lower organisms alone is found the type of reproduction in which meiosis immediately follows fertilisation, and is perhaps, as we shall see, immediately conditioned by it. In these we find both diploid parthenogenesis (*e.g.*, *Chara crinita*, Ernst, 1917 ; *Coccineis placentula*, Geitler, 1927) and haploid parthenogenesis (*e.g.*, many fungi, *Camarophyllus*, Bauch, 1926 ; *Schizophyllum*, Kniep, 1927 ; *Saprolegnia*, Mäckel, 1928).

3. NON-RECURRENT APOMIXIS

The omission of one of the two essential sexual processes (meiosis and fertilisation) without the other is necessarily a non-recurrent abnormality of the life cycle, for it would otherwise lead to indefinite reduction or indefinite multiplication of the numbers of the chromosomes. Such an omission can therefore only be expected as a result of exceptional conditions, whether genetic or external, whether natural or artificial—if the distinction can be made. These kinds of conditions have often been found. Of the three types of result, one, the formation of unreduced gametes, especially in hybrids, is of great importance in the origin of polyploids. It has been considered in relation to abnormalities of meiosis (Ch. XIII).

(i) **Parthenogenesis.** This abnormality, the omission of fertilisation without the omission of meiosis, has, with a few doubtful exceptions, only been observed to give mature progeny in certain flowering plants of various groups. The early stages of development of this kind have been found in some animals and in *Cutleria* (Phæophyceæ) by Yamanouchi (1912), where the female gametophyte was protected from fertilisation. The egg-cell develops without fertilisation into the embryo sporophyte. The development has been observed at all stages in *Solanum* (Jørgensen, 1928) ; in other cases it is inferred from the seedling being of a reduced size and having the reduced chromosome number and external character of one parent. The following list tabulates the evidence of this kind in the twenty known examples. In the last five, the seedlings resembled their male parent and had half its chromosome number, so that the inference was drawn that a generative nucleus of the pollen entered the egg-cell, whose nucleus died while the pollen nucleus gave rise to the embryo. This " male parthenogenesis "—or, it might be said, cuckoo-parthenogenesis—is analogous to that stimulated artificially in *Vaucheria* (v. Wettstein, 1919), and in echinoderms, where it is possible to " fertilise " an artificially enucleated egg fragment.

Crane and Jørgensen have produced haploid plants of *Solanum nigrum* by inducing parthenogenesis in two ways : (i) a periclinal chimæra of one layer of *S. sisymbrifolium* over *S. nigrum* var. *gracile* was self-pollinated. Owing, it is believed, to the purely *nigrum* pollen grains growing less satisfactorily in the chimæra, few ovules were fertilised ; others, apparently stimulated by the pollination, developed parthenogenetically. One haploid plant was raised : it was a dwarf *S. nigrum* in character ; (ii) ninety flowers of *S. nigrum* were pollinated by *S. luteum* and yielded 43 fruits with 70 seeds, of which 35 germinated ; 7 were haploid, and the remaining 28 diploid. All were maternal in character. Genetical evidence later pointed to somatic doubling of the chromosome number at an early stage in the parthenogenetic embryos and not to failure of reduction, as the explanation of the origin of the diploid progeny. Similar evidence

Table 62

Cases of Non-Recurrent Parthenogenesis in the Angiosperms

Species of True Parent.	Chromosome Numbers.		Ostensible Male Parent.	Author.
	Parent.	Offspring.		
A. Female Parthenogenesis.				
1. *Datura Stramonium* ($2x$)	24	12	Self or *D. ferox*.	Belling and Blakeslee, 1923.
2. *Nicotiana Tabacum* ($4x-1$)	47	24	*Nicotiana sylvestris*	Clausen and Mann, 1926.
3. *Triticum compactum* ($6x$)	42	21	*Ægilops cylindrica*	Gaines and Aase, 1926.
4. *Campanula persicifolia* ($4x$)	32	16	*Campanula persicifolia* ($2n$)	Gairdner, 1926.
5. *Œnothera Lamarckiana gigas* ($4x$)	28	14	Self	Håkansson, 1927.
6. *Crepis capillaris* ($2x$)	6	3	*C. tectorum* ($2n = 8$)	Hollingshead, 1928 *a*.
7. *Solanum nigrum* ($6x$)	72	36	*S. luteum* ($2n = 48$)	Jørgensen, 1928.
8. *Matthiola incana* ($2x$)	14+1	7+1	Self (plant with extra small chromosome).	Lesley and Frost, 1928.
9. *Solanum Lycopersicum* ($2x$)	24	12	Self	Lindstrom, 1929.
10. *Œnothera franciscana* ($2x$)	14	7	Self	Davis and Kulkarni, 1929.
11. *Œnothera* sp.	14	7	*Œ. franciscana sulfurea*	Emerson, 1930.
12. *Œnothera rubricalyx* ($2x$)	14	7	*Œ. eriensis*	Gates and Goodwin, 1930.
13. *Nicotiana glutinosa* ($2x$)	24	12	Self	Goodspeed and Avery, 1930.
14. *Digitalis purpurea* × *D. ambigua* ($4x$) (= *D. mertonensis*)	112	56	*D. ambigua* ($2n = 56$)	Buxton and D. (*cf*. Ch. IX).
15. *Œnothera franciscana* ($2x$)	14	7 and 14	*Œ. longiflora* ($2n = 14$)	Stomps, 1930 *a*.
16. *Œ. Hookeri* ($2x$)	14	7	(i) *Œ. longiflora* (ii) *Œ. argillicola* ($2n = 14$)	
17. *Œ. argillicola* ($2x$)	14	7 (16 plants)	*Œ. biennis* ($2n = 14$)	Stomps, 1930 *b*.

18. *Œ. biennis gigas* (4*x*) . . .	28	14	*Œ. biennis gigas cruciata* .	Stomps, 1928, 1931.
19. *Œ. franciscana lata* (2*x* + 1, *ex* haploid).	15	7	Self (8 plants haploid in 178)	Stomps, 1931.
20. *Œ. Lamarckiana blandina* (2*x*) .	14	7*	*Œ. longiflora* . . .	,, ,,
21. *Œ. Lamarckiana* (2*x*) (mutating to *blandina*).	14	7*	Self	,, ,,
22. *Fragaria vesca* (2*x*) . . .	14	14†	*F. chilænsis* ($2n=8x=56$) .	East, 1930.
23. *Oryza sativa* (2*x*) . . .	24	12 and 24	Dwarf variety . . .	Morinaga and Fukushima, 1931.

Species of True Parent.	Chromosome Numbers.		Ostensible Female Parent.	Author.
	Parent.	Offspring.		
B. MALE PARTHENOGENESIS.				
24. *Nicotiana Langsdorffii* . .	18	9	*N. Tabacum* . . .	Kostoff, 1929.
25. *Nicotiana Tabacum* . . .	48	24	*N. Tabacum* × *N. glutinosa*	Clausen and Lammerts, 1929.
26. *Fragaria virginiana* . . .	28	28	*F. vesca* (*rosea* × *alba*) ($n = 7$).	Ichijima, 1930.
27. *Vicia sativa*	12	12*	*Lens esculenta* ($n = 7$) .	Bleier, 1929.
28. *Euchlæna mexicana* . . .	20	20* †	*Tripsacum dactyloides* ($n = 36$).	Collins and Kempton, 1916.

* Numbers presumed on good grounds.

† Evidently somatic doubling has occurred. In *Fragaria vesca* seedlings showed segregation of recessive characters (East, 1930).

N.B. Only structurally homozygous diploids give parthenogenetic seedlings, and those polyploids whose chromosomes have approximately identical mates.

shows that such haploid parthenogenesis followed by doubling is probably very common when interspecific crosses are made in *Fragaria* and *Nicotiana* (East, 1930), and it may reasonably be supposed that these observations are of general significance in the flowering plants.

When the embryo-sacs of *S. nigrum* were examined after cross-pollination with *S. luteum*, it was found that one or both of the generative nuclei of a pollen grain had often entered an egg-cell and later degenerated, as in artificial parthenogenesis, in the echinoderms. Probably in the same way the egg-cell nucleus degenerates in the occurrence of male parthenogenesis.

The *Triticum* haploid plant arose from an exceptionally large seed—the opposite of what would be expected if the pollen played no part in its development. This suggested to Gaines and Aase that its origin was due to both the generative nuclei of the pollen fusing with the central nucleus to give a tetraploid instead of a triploid endosperm nucleus.

The fifty *Datura* haploids (*cf.* Blakeslee, Morrison and Avery, 1928) owed their origin to the stimulation of cold (*cf.* Haberlandt, 1927), or to pollination with *Datura ferox*.

We can therefore point to four conditions which lead to non-recurrent parthenogenesis in the flowering plants: (i) Exceptional external conditions (temperatures). (ii) Pollination without fertilisation or with fertilisation only of neighbouring ovules. (iii) Accidental fusion of both male nuclei with the fusion nucleus. (iv) The entry of an alien nucleus into the egg-cell without fusion. (This condition is analogous to that found in pseudogamous diploid parthenogenesis.) The three last conditions are often called forth by cross-pollination with another species, and it would appear that by this means parthenogenetic seedlings could be obtained in most groups of the dicotyledons, for they have been found wherever they have been thoroughly searched for. Therefore, although non-recurrent parthenogenesis has, for obvious reasons, been found only under experiment, there is no reason to doubt that it occurs in nature, at least in self-sterile or diœcious plants.

Nevertheless, two genetical conditions appear to limit the occurrence of non-recurrent parthenogenesis. First, the plant must be sexually fertile and homozygous or nearly so, for the conditions which eliminate the segregates of highly heterozygous organisms (such as interspecific hybrids) and lead to their sterility are much more stringent in haploid parthenogenesis, since the single gametic genotype has to meet all the conditions of life, and not merely those normal to the gamete (*cf.* Ch. IX) It is much more likely to do so if it has the same qualitative constitution as its parent, and this is only possible where the parent is homozygous. Attempts to obtain parthenogenetic seedlings of heterozygous species of *Œnothera* have therefore been unsuccessful (Davis, 1931 ; Stomps, 1931).

Secondly, a definite hereditary predisposition to produce parthenogenetic offspring is indicated in a trisomic diploid *Œnothera franciscana* ($2n = 15$), itself derived from a haploid seedling (Stomps, 1931). Such a predisposition is equally to be regarded as a condition of diploid parthenogenesis, for failure of reduction in itself is no stimulus to parthenogenesis.

In connection with non-recurrent parthenogenesis two other errors of fertilisation, both occurring under normal conditions, may be mentioned. It has been possible to show in *Drosophila,* from genetical considerations, that a single, mosaic, zygote may develop from two separately fertilised eggs sticking together (Stern and Sekiguti, 1930) and from a binucleate egg, the two nuclei of which were separately fertilised (Stern, 1927).

(ii) **Regeneration and Apospory.** By injury or by vegetative propagation it is possible to " regenerate " the gametophyte of a liverwort (Marchals, 1906, 1907) or a moss (v. Wettstein, 1924) from the diploid tissue of the sporophyte. The new gametophyte has escaped meiosis and is therefore diploid. This is artificial and necessarily non-recurrent apospory. From the diploid gametophytes tetraploid sporophytes are obtained, and by repeating this process v. Wettstein has succeeded in obtaining octoploid sporophytes. The same effect has been produced in the fern, *Osmunda* (Manton, 1932).

A more complicated condition has been found by Andersson-Kottö (1931, 1932) as a result of mutation in the fern *Scolopendrium crispum muricatum,* but being heritable the anomaly is recurrent. When the gametophytes from this plant were intercrossed (a process analogous to self-fertilising a flowering plant) one-quarter of the progeny developed the mutant character, which is therefore a mendelian recessive. The character consists in the development of gametophytic tissue on the fronds of the sporophyte. There is no spore formation or meiotic process of any kind at this stage. The gametophyte, therefore, has the diploid complement of the sporophyte. And, as in regeneration, it produces functional gametes which should yield tetraploid sporophytes in the next generation. This process is recurrent although indefinite repetition is scarcely conceivable.

When crossed with another race having the same chromosome number ($2n = 60$) the first generation was normal and its gametophytes all had 30 chromosomes. Yet these produced sporophytes all having about 45 chromosomes. By selfing the gametophytes from these plants and crossing them with normal types it was proved that the male gametes had often undergone a second reduction, to 15 chromosomes (*cf.* Manton, *l.c.*). One-quarter of the second generation were aposporous plants, and all these bred true to the character of having a redundant although apparently often imperfect meiosis. The combination of apospory with antheridial meiosis gave chromosome numbers increasing by about a half in succeeding generations, thus : F_2, *ca.* 45 ; F_3, *ca.* 65 ; F_4, *ca.* 95. These results point to the redundant meiosis being an independent hereditary character. It is analogous to the condition in the pseudo-hermaphrodite *Icerya purchasi*. The reduction to 15 indicates that the original plants were tetraploid.

The unbalanced occurrence of apospory and parthenogenesis, as well as many observations on polyploids, show that the association of change of chromosome number with the alternation of form in succeeding generations is not due to a relationship of cause and effect, but that they are, each, a genetic property of the race achieved by independent adaptation, immediately conditioned by the stage in the cycle of development, and therefore readily separable.

4. APOMIXIS IN RELATION TO MEIOSIS

(i) **Meiosis in Functional Cells in Parthenogenesis.** Where the cell which would normally undergo meiosis still enters into the life cycle (as do the oöcyte, the embryo-sac mother-cell or the spore mother-cell in diploid parthenogenesis) it is clear that meiosis must be suppressed, so far as it effects a numerical reduction of the chromosomes. The ways in which this happens may for convenience be grouped in five classes, although gradations are commonly observed between some of them (*cf.* Ch. XIII).

1. Incomplete, usually slight, pairing of the chromosomes at the first metaphase, lagging of the unpaired chromosomes at anaphase and consequent formation of a restitution nucleus. A single second division plate is formed at metaphase and a dyad of unreduced nuclei at telophase. (It is possible, on analogy with the pollen mother-cell, that the second division may be exceptionally suppressed in the same way.) This occurs in various hybrid plant species: *Marsilia Drummondii* (Strasburger, 1907), *Nephrodium hirtipes* (Steil, 1919). *Erigeron Karwinskiana* (Carano, 1921), *Balanophora japonica* (Kuwada, 1928), *Eupatorium glandulosum* (Holmgren, 1919), *cf. Raphanus-Brassica* (Karpechenko, 1927).

2. Contraction of the nucleus after an attempted pachytene or even metaphase and reappearance of the chromosomes unpaired and often uncontracted, as at mitosis, to divide once. This occurs in plants with obligatory parthenogenesis as well as in animals with facultative parthenogenesis: *Elatostema acuminatum* (Strasburger, 1910; the single division appears as the first division of the embryo-sac), *Taraxacum albidum* (Osawa, 1913), *Aphis palmæ* (de Baehr, 1919), *Cynips* and *Rhodites rosæ* (Hogben, 1920), *Artemisia nitida* (Chiarugi, 1926), probably *Ochna serrulata* (Chiarugi and Francini, 1930).

3. Complete failure of pachytene and metaphase pairing of the chromosomes, which then divide once. This also occurs with both facultative and obligatory parthenogenesis. *Elatostema sessile* (Strasburger, 1910), *Phylloxera* (Morgan, 1915), *Artemia salina* (Fries, 1909), *Rhabditis* species (Belar, 1923), various Rotifera (Storch, 1924), *Eu-Hieracium* (Rosenberg, 1917), *Chondrilla juncea* (Rosenberg, 1912), *Camarophyllus virgineus* (Bauch, 1926), *Artemisia nitida* (Chiarugi, 1926), *Lecanium hesperidum* (obligate parthenogenetic race, Thomsen, 1927). *Note*: *Zephyranthes texana* (Pace, 1913) is presumably of this type.

4. Failure of metaphase pairing followed by division of the chromosomes at both divisions : *Thismia javanica* (probably, Meyer, 1925) ; *Artemisia nitida* (Chiarugi, 1926), *Bacillus rossii* (v. Baehr, 1907), *Cocconeis placentula* (Geitler, 1927). In this form pachytene pairing was noticed, but 28 univalents appeared at metaphase instead of 14 pairs as in related forms. *cf. Pygæra* hybrid (Federley, 1913).

5. Normal prophase and first division followed by (i) failure of separation of the two bodies of chromosomes at the second anaphase ; or (ii) reunion of two daughter-nuclei at the second telophase ; or (iii) fusion of two nuclei in early somatic division of the embryo. This method is found only in animals. (i) *Rhabditis monohystera*, Nematoda (Belar, 1923), *Solenobia pineti*, Lepidoptera (Seiler, 1923). (i) or (ii) *Artemia salina*, Crustacea (Brauer, 1894 ; Fries, 1909) (three different methods have been observed here). (i) *Cypris* species, Crustacea (Woltereck, 1898). (iii.) *Solenobia triquetrella*, Lepidoptera (Seiler, 1923) ; (*cf.* Jørgensen, 1928, on *Solanum*), *Lecanium hesperidum*, Hemiptera (facultative parthenogenesis), (Thomsen, 1927). (ii) or (iii) *Apotettix*, Orthoptera (facultative parthenogenesis) (Nabours, 1931 *c*). (iii) *Trialeurodes vaporiarum*, Coccidæ (Thomsen, 1927). *Allium* (Haberlandt, 1923) is analogous, although not strictly parthenogenesis but apogamy. The genetic results differ : when the diploid number is restored by the second or third method it follows that the offspring of heterozygotes will always be homozygotes. This is so in *Paratettix* and *Apotettix*.*

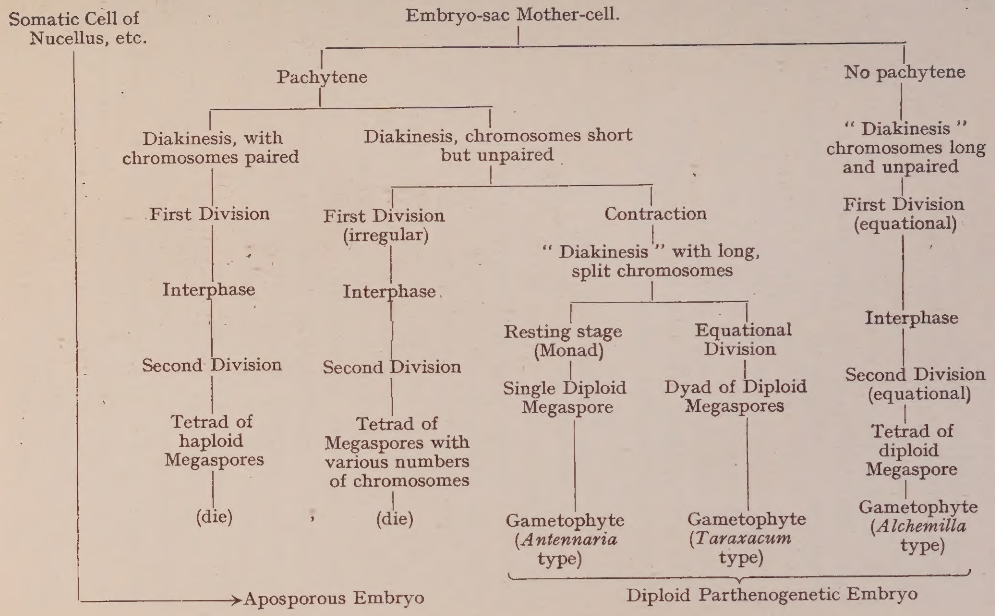
Side by side with these *regular* abnormalities others occur, particularly in the spore mother-cells of aposporous plants, but also sometimes in those reproducing facultatively by diploid parthenogenesis. The irregularities consist in the characteristic results of failure of pairing in hybrids—irregular distribution of the

---

* The facultatively parthenogenetic Orthoptera, *Apotettix* and *Paratettix*, are probably of the last type (Robertson, 1930). Here the suppression of meiosis is correlated with the association side by side of the corresponding pairs of chromosomes in the somatic divisions of the offspring. This is unparalleled in its closeness, for the chromosomes appear to behave as a unit both at metaphase and anaphase. The association gradually disappears in the course of development. In the absence of direct observations on the suppressed meiosis of the parents the relation of these observations to the suppression, or to the phenomenon of somatic pairing, cannot be determined.

TABLE 63

Methods of Apomixis in *Artemisia nitida*


Somatic Cell of Nucellus, etc.
Embryo-sac Mother-cell.
Pachytene
No pachytene
Diakinesis, with chromosomes paired
Diakinesis, chromosomes short but unpaired
" Diakinesis " chromosomes long and unpaired
First Division
First Division (irregular)
Contraction
First Division (equational)
" Diakinesis " with long, split chromosomes
Interphase
Interphase
Interphase
Resting stage (Monad)
Equational Division
Second Division
Second Division
Second Division (equational)
Single Diploid Megaspore
Dyad of Diploid Megaspores
Tetrad of haploid Megaspores
Tetrad of Megaspores with various numbers of chromosomes
Tetrad of diploid Megaspore
(die)
(die)
Gametophyte (*Antennaria* type)
Gametophyte (*Taraxacum* type)
Gametophyte (*Alchemilla* type)
Aposporous Embryo
Diploid Parthenogenetic Embryo

chromosomes at either the first or the second division, and formation of numerous daughter-nuclei (*Artemisia nitida, Nephrodium hirtipes*). Diploid parthenogenesis is out of the question in the cells affected, just as it would be following normal reduction, which is occasionally to be observed in certain plants that are obligatorily apomictic (*Artemisia nitida* ; *Ochna serrulata*). Regular reduction is always to be found in those that are facultatively sexual (*e.g.*, *Elatostema sessile* and *Allium odorum*, Modilewski, 1931). Plants that are apogamous or aposporous and not parthenogenetic (*Hieracium pilosella, Citrus*, probably *Rosa canina* are nearly always facultatively sexual and therefore have, as a rule, regular meiosis. The *Caninæ* roses, for example, have a meiosis which is not normal but which is regular in effect (Ch. XIII).

The great range of behaviour that is possible in certain apomictic plants and its relation to the course of meiosis is shown by *Artemisia nitida* (Table 63).

(ii) **Meiosis in Non-Functional Cells.** The mother-cells of male spores and male gametes of apomictic plants and animals (where they are formed) show various kinds of behaviour which cannot be predicted merely from a knowledge of the behaviour in the functional cells on the female side although the two show a certain correlation. They have been studied more thoroughly than the functional cells and provide valuable evidence of the origin of apomixis.

All facultatively apomictic plants have normal or fairly normal meiosis in the pollen mother-cells, *e.g.*, *Alchemilla speciosa* (Murbeck, 1902), *Thalictrum purpurascens* (Overton, 1904), *Hieracium aurantiacum* (Rosenberg, 1917), *Elatostema acuminatum* (Strasburger, 1910)—here the pollen degenerates afterwards, as in so many male-sterile plants. They are able to produce gametes with a normally reduced chromosome number.

In some organisms which are obligatorily parthenogenetic the male cells function in stimulating parthenogenesis ; their meiosis is then fairly regular. In *Zephyranthes texana* it is entirely so, and the pollen actually functions in fertilising the endosperm nucleus. Moderate or even high pollen fertility is sometimes found in the pseudogamous *Potentilla* species. In spermatocytes produced in the ovary of a parthenogenetic *Rhabditis* (Belar, 1923) meiosis is also not completely irregular; some pairing of chromosomes is found at the first metaphase, and the sperm formed actually functions in stimulating the egg to development.

Amongst species with obligatory apomixis we have every reason to believe that the pollen mother-cell behaviour is closely parallel with that in the embryo-sac mother-cell, except that the purely mitotic *Antennaria* and *Eu-hieracium* type of development is missing. Two groups must be distinguished: (i) Species with apospory or nucellar embryony as well as parthenogenesis. (ii) Species that are solely parthenogenetic.

The first are naturally less dependent on the regular formation of diploid gametes (for the embryo-sac) and it is found that while meiosis is often suppressed owing to the reconstitution of a single nucleus at the first telophase (following the lagging of a variable number of unpaired chromosomes) yet often the results are entirely irregular or a tetrad is formed of nuclei with different numbers of chromosomes. This is the case in *Erigeron annuus*, *Artemisia nitida* and *Ochna serrulata*. In the last species pairing follows precisely the frequencies observed in the sterile autopolyploid *Tulipa Clusiana*, which is also a pentaploid (Figs. 60-62).

In purely parthenogenetic species (*e.g.*, *Eu-hieracium*) meiosis is rather more regularly suppressed. But several gradations have been described by Rosenberg in this apparent transition towards the regular formation of diploid gametes (if we may infer a progressive change). In all these the early prophase appears normal, and doubtless some association of chromosomes occurs at pachytene. The first stage of "degeneration" corresponds with that found in such hybrids as *Raphanus-Brassica*. Few (in *Hieracium boreale* and *Chondrilla juncea*, with embryo-sac of type 1) or no chromosomes (in *Hieracium lævigatum*, with embryo-sac of type 2) are paired and very often, probably as a result of the uneven distribution and lagging of the unpaired chromosomes on the spindle, a single resting interphase nucleus is reconstituted before the two groups are clearly separated. This "restitution nucleus" divides to give daughter-nuclei, each of which has the unreduced number of chromosomes. Various abnormalities occur, such as the formation of one or more, usually small, supernumerary nuclei (Fig. 105).

The second stage of degeneration is found in *H. pseudoillyricum* and a few other species (with embryo-sac of type 3). The nucleus contracts after reaching a stage immediately before diakinesis, and on resuming its prophase condition develops directly into a somatic mitosis and gives a dyad. This type of division is often found together with the *lævigatum* type, for variations always occur in the same individual, as they do in all other irregular chromosome behaviour (Rosenberg, 1927).

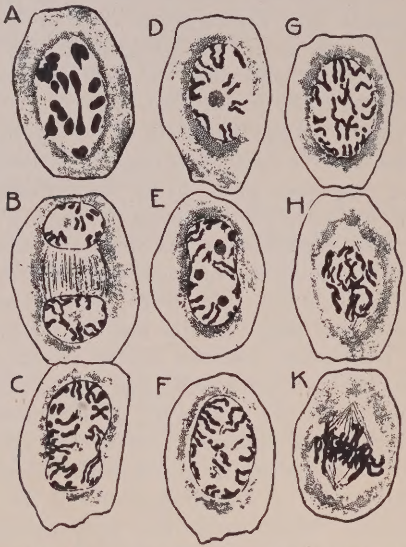


FIG. 105.—Meiosis in pollen mother-cells of *Hieracium boreale* ($3x = 27$). A, metaphase with two bivalents and the remaining chromosomes univalent (described as a "semi-heterotypic" metaphase). B, telophase with separation of two nuclei. C–G, restitution nuclei formed at telophase. H and K, single second division, with the unreduced number of chromosomes; this will yield a dyad of pollen-grains. (After Rosenberg, 1927.)

All such variation may be explained by saying that environmental and developmental variations have a certain threshold value in the effect on the general course of meiosis in a sexually fertile organism (they can only be detected by their effect on chiasma frequency), while in hybrids and organisms with genetically abnormal meiosis there is no such threshold value.

(iii) **Meiosis in Haploids.** The occurrence of meiosis in a mother-cell is affected in an entirely different way by haploidy according as the fertilisation which has failed is normally premeiotic or post-meiotic. The first type has been found in algæ and fungi, the second in the angiosperms (Ch. XIII), and in animals with haplo-diploid sex differentiation.

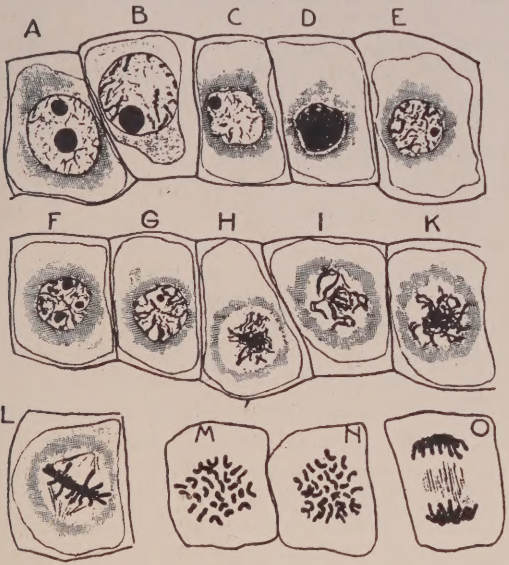


FIG. 106.—Meiosis in pollen mother-cells of *H. pseudoillyricum* ($3x = 27$). A–C, early prophase. D, contraction replacing first division. E–G, renewed prophase of second division. H–O, second division which gives dyad of pollen-grains with the unreduced chromosome number. (After Rosenberg, 1927.)

In *Vaucheria hamata* (v. Wettstein, 1920) it is possible to stimulate both male and female gametes to development without fertilisation or the meiosis which would normally follow it. Parthenogenesis can be similarly induced (by treatment with dilute solutions) in *Spirogyra, Ulothrix,* and *Saprolegnia mixta* (Mäckel, 1928).

In the sexual basidiomycetes the conjugating nuclei fuse in the basidial cell and immediately undergo meiosis. The four daughter-nuclei then pass into the four terminal sacs, where they develop into spores. But in some species only two sacs are produced, and in these it is believed that two nuclei pass into each (Sass, 1929). In parthenogenetic species the single nucleus of the basidial cell divides once where two sacs are developed (*Camarophyllus virgineus*, Bauch, 1926, *v.* Fig. 107), and twice where four sacs are developed (*Schizophyllum commune*, Kniep, 1928, p. 422). These observations are paralleled in the Uredineæ (*cf.* Rosenberg, 1930).

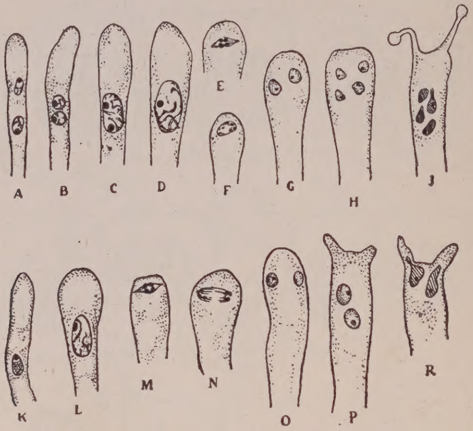


FIG. 107.—Spore-formation in the sexual four-spore (A–J) and the non-sexual two-spore (K–R) race of *Camarophyllus virgineus*. A, paired, diplophase nuclei. B, C, their fusion. D, zygotene. E, metaphase of the first division. F, anaphase. G, interphase. H, telophase of second division. J, migration of the four nuclei into their pouches. K, single nucleus. L, prophase. M, N, single division. O–P, spore nuclei formed. R, their migration. (From Rosenberg, 1930, after Bauch, 1926.)

Thus, in forms where fertilisation immediately precedes meiosis, the omission of fertilisation means, sometimes, the suppression of meiosis, *e.g.*, in the parthenogenetic race of *Camarophyllus virgineus*, Bauch (1926) found early prophase stages reminiscent of meiosis, although the later course of the single division in the basidium was purely mitotic ($n = 4$). Elsewhere there appears to be a complete absence of any meiotic process, and the nucleus instead divides mitotically twice, once or not at all as purely vegetative conditions dictate (*Vaucheria*, v. Wettstein, 1920). Habitual parthenogenesis can therefore be induced (artificially or by mutation) at one step in such an organism as *Chara crinita*, while in diploid organisms the assumption of parthenogenetic habit must necessarily be more complicated, since it means a change in a specialised meiotic mechanism (*v.* p. 458).

In haploids derived from organisms with a prolonged diploid generation two types of meiosis are found according as the haploidy is habitual (in certain male Hymenoptera and in coccids) or adventitious (in angiosperms arising by parthenogenesis from diploid parents). In both the chromosomes are contracted as in ordinary meiosis, but, of course, unpaired. In the drone bee (*Apis*, Meves, 1907) a spindle is formed and the chromosomes lie on a metaphase plate but do not divide; at one pole an enucleate bud is cut off, a second division spindle is formed and the chromosomes divide this time to give two daughter-nuclei, one of which is extruded as a polar body while the other gives a haploid (unreduced) spermatozoon.

In the haploid male coccids (*Icerya*, etc., $n = 2$; Hughes-Schrader, 1930) only one division occurs, and it is not clear whether this corresponds to the first or the second. In the haploid male rotifers (*Asplanchna*, $n = 13$; Whitney, 1929) it is the second division that is usually omitted; where an abortive second division occurs spermatozoa are formed with less than the haploid number, and these do not function. The mechanism is apparently imperfect.

This suppression of meiosis seems to be a sexual characteristic not directly determined by the haploid condition. Diploids sometimes show the male character in the hymenopteran *Habrobracon*, and genetic evidence shows that these produce diploid sperm (Torvik, 1931). They presumably have the abortive meiosis characteristic of males. This shows that the mechanism of meiosis is here genetically adapted to give regular failure of reduction. The condition of the adventitious haploids in the angiosperms, on the other hand, is different. The ordinary meiotic mechanism has to deal with unpaired chromosomes, and the result is irregular (*v*. Ch. XIII).

Such observations also show that where meiosis takes place at the end of the diploid generation there is a mechanism of division external to the chromosomes and distinct from that of ordinary mitotic division (*cf*. Ch. XIII). In the adventitious haploid angiosperms we see it acting on unpaired chromosomes, for whose division it is unadapted. In the haploid Hymenoptera we see it specially adapted to deal with the situation so as to produce regular results.

In the organisms in which meiosis immediately follows fertilisation, on the other hand, there is no evidence of any such mechanism. Since every cell in these which is diploid undergoes meiosis it seems possible to consider that meiosis, which in the higher organisms must be regarded as induced in specialised cells by their relationship with the rest of the organism, is in these simple forms determined directly by the condition of diploidy (*v*. Chs. XI and XVI). In this connection the parthenogenetic *Chara crinita*, Ernst, 1917) is of interest. It is diploid, unlike its sexual relations ; but since, as Ernst supposes, it is probably a hybrid, the normal diploid condition, the presence of pairs of identical chromosomes, is lacking. Parthenogenesis will therefore follow the failure of meiosis in such an individual as a matter of course, if it happens to be female like the regenerated diploid gametophytes of *Sphærocarpus* (Lorbeer, 1927). Hybridity is then seen as a simple and immediate condition of parthenogenesis.

(iv) **Meiosis in Cyclical Parthenogenesis.** Males arise in the cyclically parthenogenetic Rotifers, as they do in the Hymenoptera, presumably by haploid parthenogenesis. In the aphids and phylloxerans it has been established (*cf*. Morgan, 1912, 1915) that the development of males is due to the loss of one chromosome (an X chromosome) at maturation in the egg of the parthenogenetic mother. The $2x-1$ males might be expected to give offspring like themselves as well as females, but the true-breeding parthenogenetic line is restored by the functioning of only those sperms with the full haploid number.

The same aberration occurs less regularly in the Orthoptera. In *Apotettix* and *Paratettix*, Robertson (1930, 1931 *c*) found that the males exceptionally produced by parthenogenetic females lacked one of the *X* chromosomes of their parents, as do the normal males in the grasshoppers. This was supposed to be the result of non-disjunction, probably conditioned by a special property of the *X* chromosomes. Such property as, for example, that of precocious development found in the single *X* chromosomes in the male might affect its pairing if equally present in the female, and hence lead to lagging and loss (*v*. Ch. XIV and p. 361).

5. THE ORIGIN OF APOMIXIS IN EXPERIMENT

The foregoing account has shown the characteristics of nuclear behaviour in apomixis. Apart from these immediate conditions certain events external to the nucleus can be related to the occurrence of apomixis as prior conditions. First we may note that the variations in conditions which are responsible for the change from sexual to parthenogenetic reproduction may be imposed artificially (*cf*. Nabours, 1919 on *Paratettix* and *Apotettix*).

(i) **Pseudogamy.** In some species of plants and animals the male gamete functions in exciting the development of the unfertilised and unreduced egg in diploid parthenogenesis or of nucellar embryos in apospory. This is known as pseudogamy. We have already seen how non-recurrent parthenogenesis is stimulated in plants in this way.

In a nematode, *Rhabditis* "*XX*," Belar (1923) found that the sperm, although irregularly formed (in part of the ovarian tissue), entered the egg and stimulated its development, probably by the contribution of its centrosome—the middle-piece of the sperm—although no fusion occurred.

An analogous process is found in various monocotyledons, *e.g.*, *Zephyranthes texana* and *Allium odorum* (Modilewski, 1930). Here the pollen is normally developed and one generative nucleus fuses with the central nucleus to give the endosperm; the other degenerates, but the first fusion stimulates the development of the unreduced egg-cell. Pollination is also necessary to stimulate apogamy and apospory in *Allium odorum* (Haberlandt, 1923) and *Zygopetalum* (Suessenguth, 1923).

In *Potentilla* (Müntzing, 1928) several species which fail to set seed without pollination produce entirely maternal offspring when cross-pollinated, as well as when self-pollinated. Some of these species have good pollen, others bad. In *Rubus* (Lidforss, 1914; Gustafsson, 1930) the position is more complicated. In many European species of blackberries (section *Eu-batus*) crosses with closely related forms yield a high proportion of hybrids, crosses with more distant species yield entirely maternal offspring—" false hybrids." These are identical with the female parent, yet when such plants are selfed they yield the heterogeneous progeny characteristic of a sexually reproducing hybrid. Evidently the proportion of sexual embryos diminishes with increasing remoteness of the male parent. Such a situation indicates competition between the sexual embryos and their substitutes, the asexual, probably aposporous, ones. The same conditions probably apply to the *Caninae* roses, although the evidence here is still scanty (Hurst, 1931), and to Ohmachi's orthopteran hybrids (1929 *b*).

Thus pseudogamy may stimulate either apospory (in *Allium*, probably in *Rosa* and *Potentilla*) or diploid parthenogenesis (*Rhabditis*, *Zephyranthes*).

(ii) **Injury.** By electrical, chemical and mechanical stimuli the unfertilised egg has been induced to develop in many Echinoderma and Algæ, in the frog and elsewhere. Where the stimulus is applied after the two polar bodies have been extruded from the animal egg a haploid embryo develops. In the frog, where this has happened, somatic doubling has followed later as in the somatic origin of polyploid plants and in some kinds of diploid parthenogenesis. The general failure of a diploid organism produced in this way to reach maturity is probably due to the presence in most outbred organisms of factors lethal in the homozygous condition. The same result is obtained when a sperm fertilises an enucleated egg (" male parthenogenesis "). Where reduction has not taken place the stimulus may lead to the suppression of one of the meiotic divisions or to the fusion of the products of the second meiotic division (as in the production of diploid spores of *Funaria* by v. Wettstein, 1924).

An embryo may then develop without fertilisation. Such individuals do not usually get beyond an early stage of development.

It is possible to induce the direct development of an unfertilised gamete in many Algæ where meiosis should immediately follow fertilisation, in various ways. Thus when the antheridia or oögonia of *Vaucheria hamata* (v. Wettstein, 1919) were pricked they developed directly into new thalli : both fertilisation and meiosis were omitted. Apospory was induced by layering the fronds in *Nephrodium* (Digby, 1905). This automatically led to apogamy.

The development of adventitious embryos from the nucellus or integument has been induced by wounding in *Œnothera Lamarckiana* by Haberlandt (1921 *a*). He also found that degeneration of the nucellar tissue and synergids was associated with parthenogenesis in *Taraxacum* and *Hieracium*, while in sexual species of *Hieracium* no such degeneration occurred (1921 *b*). These observations make it plausible that degeneration of neighbouring tissue may stimulate apospory and parthenogenesis, and thus be a prior, and genetically determined, condition of these phenomena.

(iii) **Mutation.** Paula Hertwig (1920) found a sexual strain of *Rhabditis pellis* which gave rise to a purely parthenogenetic strain which bred true to the new character. It has the same chromosome number as the parent race, but its egg-cells underwent a single division at meiosis and gave unreduced eggs. The entrance of the sperm was necessary to stimulate development without fertilisation, as in the related parthenogenetic species. In this case parthenogenesis must be regarded as a genetic character arising by mutation.

(iv) **Hybridisation.** Ostenfeld (1910), by crossing facultatively sexual species of the Pilosella section of *Hieracium*, with purely sexual species, *e.g.*, *H. aurantiacum* × *H. auricula*, produced a heterogeneous progeny of three types : (i) sterile ; (ii) purely asexual, probably aposporous ; and (iii) asexual when self-pollinated, sexual when crossed with good pollen. When we consider this in relation to Lidforss's observations on *Rubus* we see that with plants having the genetic faculty of producing aposporous offspring, the greater their hybridity the less the chance of their successfully producing sexual offspring—owing to the sterility inherited as a concomitant of high segregation—and therefore the greater the proportion of asexual seedlings produced on self-fertilisation. The extreme type, being sexually sterile, will be obligatorily apomictic. But in the same group we find plants not having the faculty of apomixis and sexually sterile as well.

Harrison (1920) crossed two sexual species, *Tephrosia crepuscularia* and *T. bistortata* (Lepidoptera) and obtained four parthenogenetic females amongst normally sexual progeny. When this happened on a second occasion the offspring of the parthenogenetic female showed segregation of recessive characters (Peacock, 1925). This should happen with the kind of parthenogenesis found by Seiler in the Lepidoptera. Seiler (1927) crossed parthenogenetic and sexual races of *Solenobia triquetrella*, and the progeny showed variation in behaviour between the normal and that obtaining in the parthenogenetic race, where pairs of nuclei fused after the second segmentation division in the embryo. There were various other irregularities, with the result that different individuals and parts of individuals had different numbers of chromosomes.

(v) **The evidence of Chromosome Numbers.** It was early noticed that apomictic species of flowering plants had, as a rule, higher chromosome numbers than their sexual relatives. The following lists, giving the somatic chromosome numbers, show that this is still true of parthenogenetic as well as of aposporous species :—

TABLE 64

Chromosomes Numbers of Apomictic Species

DIPLOID SPECIES

Chondrilla juncea (14–16)	Rosenberg, 1912.
Zephyranthes texana (24)	Pace, 1913.
Allium odorum (16)	Haberlandt, 1923.
Potentilla argentea forma (14)	Müntzing, 1928.

TRIPLOID SPECIES

Hieracium boreale (27)	Rosenberg, 1917, 1927.
H. pseudoillyricum (27)	
H. lævigatum (27)	
H. tridentatum (27)	

Erigeron annuus (27)	Holmgren, 1919.
Eupatorium glandulosum (51)	
Artemisia nitida (37)	Chiarugi, 1926 (*cf.* Weinedel Liebau, 1930).
Taraxacum officinale (24)	Juel, 1900 ; Gustafsson, 1932.
Nothoscordon fragrans (24)	Messeri, 1931.

Tetraploid Species

Thalictrum purpurascens (48)	Overton, 1909.
Elatostema sessile (32)	Strasburger, 1910.
Hieracium boreale forms (36)	Rosenberg, 1917, 1927.
H. aurantiacum (36)	
H. Pilosella (36)	
Taraxacum croceum, etc. (32)	Gustafsson, 1932.
Antennaria alpina (52)	Juel, 1900.

Pentaploid Species

Rosa canina, etc. (35)	Täckholm, 1920, 1922.
Potentilla argentea forma (35)	Müntzing, 1928.
P. Tabernæmontana (35)	
Ochna serrulata (35)	Chiarugi and Francini, 1930.
Taraxacum spp. (45)	Osawa, 1913 ; Gustafsson, 1932.

Hexaploid Species

Potentilla collina (*ca.* 42)	Müntzing, 1928.
Allium roseum var. *bulbilliferum* (48) (viviparous).	Messeri, 1931.

The chromosome numbers show that polyploidy and particularly odd numbered polyploidy favours apomixis. Two reasons suggest themselves for this : (i) Meiosis is less regular in polyploids than in diploids, for the reason that a too great likeness of the chromosomes is here as serious a cause of irregularity as a too great dissimilarity (*cf.* D., 1928). (ii) All odd-numbered polyploids are numerical hybrids with inherent irregularity of meiosis. Nearly all triploids that have been examined, for example, form restitution nuclei

TABLE 65

Cases of Polyploidy within the Species Associated with the Occurrence of Apomixis

	Sexual (haploid-diploid).	*Apomictic* (somatic number)	Authority.
CHAROPHYTA			
Chara crinita	12–24	24	Ernst, 1917.
ANGIOSPERMA			
Potentilla argentea	—	14, 42, 56	Müntzing, 1931.
P. collina	—	35, 42	,, ,,
P. Cranzii	—	42, 49	,, ,,
P. Tabernæmontana	—	42, 84	,, ,,
Nigritella nigra	19–38	? 76	Afzelius, 1928. Chiarugi, 1929.
Hieracium umbellatum	9–18	27	Rosenberg, 1927.
Crepis acuminata	—	33, 44, 55 ?	Hollingshead and Babcock, 1930.
C. gracilis	—	22, 55 ?	,, ,, ,,
C. occidentalis	—	22, 44	,, ,, ,,
C. barbigera	—	44, 88	,, ,, ,,
Festuca ovina	7–14 21–42	14, 21, 28, 35	Lewitsky and Kuzmina, 1927. Turesson, 1930, 1931.
		(increasing in vivipary in higher numbers).	
Allium odorum	8–16	16, 24, 32	Haberlandt, 1923 (nucellar). Messeri, 1930 (nucellar) Modilewski, 1930 (diploid parthenogenesis, facultative).
A. roseum	8–16	48	Messeri, 1931 (viviparous).
INSECTA			
Solenobia pineti	30–60	120	Seiler, 1923.
S. triquetrella	30–60	120	,, 1923, 1927. (diploid and tetraploid in these two yield viable hybrids.)
CRUSTACEA			
Trichoniscus provisorius	8–16	24	Vandel, 1928.
Artemia salina	21–42	84	Artom, 1928.
Daphnia pulex	4–8	24	Schrader, 1925.

NOTE.—No other animal polyploids are known except in the hermaphrodite *Helix pomatia* ($n = 12$ and 24, *cf*. Wilson, 1925), and in experimental material of *Drosophila*. Polyploidy may be inferred very generally in the Annelida and Mollusca from a comparison of chromsome numbers in different species.

whether they are the product of hybridisation of two species or of self-fertilising a diploid.

High chromosome number (polyploidy) therefore favours the conditions both of diploid parthenogenesis (by suppression of meiosis) and apospory (by irregularity of meiosis). Taking this into consideration, together with the fact that half the species of angiosperms are polyploids, the relative frequency is intelligible.

The reason for the association of a doubling of chromosome number with parthenogenesis in *Chara crinita* (Ernst, 1917), *Artemia salina* (Artom, 1928 *et al.*), *Solenobia triquetrella* (Seiler, 1927), and *Trichoniscus provisorius* (Vandel, 1927) is fairly clear. Polyploidy has prevented fertilisation, and therefore parthenogenesis has been a condition of their survival.

The bearing of these observations on the theory of the origin of apomixis will be considered in the next chapter.

CHAPTER XVI

THE EVOLUTION OF GENETIC SYSTEMS

The Origin of Chromosomes and Mitosis—Meiosis—The Origin of Sexuality—Sexual Differentiation and Balance—The Development of the Haplo-Diploid System—The Stabilisation of Hybridity—Apomixis—The Complex-Heterozygote—Species and Variation—Principles of Evolutionary Change.

> . . . nil ideo quoniam natumst in corpore ut uti possemus,
> sed quod natumst id procreat usum.*
> LUCRETIUS, *De Rerum Natura*, IV, 834–835.

1. PREMISES

JUST as the inorganic world can be described in terms of the shape and of the movements of its constituents—and each description have its special value—so the organic world can be described in terms of the form and of the movements (or functions) found in mature or immature organisms; and in considering organic evolution these different methods have their use. But we are now in a position to consider the organic world from a new point of view, the point of view not of the organism itself but of its hereditary materials and mechanism. We can consider the evolution of the genotype as well as that of the phenotype—using these terms in a concrete sense. The difference in method is more profound than would appear, for two reasons: first, the order of structure concerned is entirely different in genotype and phenotype; secondly, they have a mutual relationship which is by no means reciprocal, for while variation in the genotype determines that in the phenotype, variation in the phenotype merely restricts the direction of that in the genotype, owing to the elimination of unfavourable genetic combinations.

The evolution of the genotype should, moreover, be of special significance because the steps in its development are relatively few and they are readily defined; the uniformity of its materials, the genes, and of their organisation in the chromosomes, compels a uniformity of change which results in parallelism in groups as widely separated as insects and angiosperms. The systematics of the genotype therefore transcend all customary classification, and changes which are believed to have occurred at remote, chiefly pre-Cambrian, periods can still be inferred from analogy with observations in experiment. For this purpose analogy with remote groups is valid on account of the great uniformity of principle in the behaviour of genetic systems. And finally there are many problems of chromosome form and action that can be resolved only on evolutionary principles. Groups of phenomena which in the past have been explained on a *unitary* hypothesis can be more usefully arranged and co-ordinated in terms of an evolutionary hypothesis. For these reasons it will be seen that the inferences to be made, although of course tentative, are often less speculative than those drawn from the comparative morphology of the phenotype.

---

* . . . for nothing is born in the body in order that we may use it, but rather, having been born, it begets a use.

The inferences must be founded on elementary physical and chemical principles, on the theory that important changes are largely of an adaptive character (leaving the question open for the moment of whether they arise under a Lamarckian stimulus or merely survive under a Darwinian selection), and on our knowledge of the structure, interactions and behaviour of the hereditary materials. This knowledge is implied by four hypotheses that have been discussed earlier; they may be restated for our present purpose as follows:—

The Theory of the Permanence of the Chromosomes. The chromosomes have a persistent structure, *i.e.*, they consist essentially of constant materials, constantly arranged; and when they multiply they do so by reproducing an identical structure.

The Chromosome Theory of Heredity. The hereditary properties of the organism, its genotype, are determined by the joint reaction of the permanent materials, the genes in the chromosomes. These properties express themselves in development by a series of interrelated reactions with the environment.

The Theory of Genotypic Control of Chromosome Behaviour. The movements, aggregation, dispersion and relation with accessory materials of the chromosomes are controlled by the reaction of the genotype and of the environment with them. This unitary control is essential to the development of any regular system adapted to the needs of reproduction. It means that the chromosomes are an integral part of the " organism as a whole," reacting with the properties of the whole which they themselves jointly determine (D., 1932 *a*).

The Theory of Mutation and Differentiation. The genes of any one organism and the genes of different organisms differ, and the difference arises by the same kind of change, *i.e.*, from one chemical entity into another. This is gene-mutation. The joint reaction of the genes may be altered by these changes and also by changes in proportion of those already present.

The Theory of Structural Change and Crossing-over. The genes are arranged in a linear order which is liable to change either from undefined causes or from a special association with homologous genes at the prophase of meiosis.

These hypotheses, together with more special considerations, cover our knowledge of the external and internal mechanics and physiology of the chromosomes and set a necessary limit to any evolutionary speculations about the chromosomes. Attempts are constantly being made to discover the meaning, function, cause or purpose of one or other of the processes discussed here. Such isolated syntheses have usually been made in advance of an analysis, for which purpose deduction from all the principles given is necessary. Several of these have only recently become clear, and by their general application a more profitable survey can be expected than hitherto.*

2. THE CHROMOSOMES AND MITOSIS

(i) The Naked Gene : Reproduction and Mutation. The original living particles must have consisted of molecules or groups of molecules capable of determining the formation of similar particles in their neighbourhood. They must also, since they gave rise to different derivatives, have had the property of occasionally reproducing dissimilar particles. These two properties, which are the basis of heredity and mutation, are both inherent in what Haldane describes as copying: a good copy gives permanence, a bad copy, mutation. Since they are characteristic of the unit of inheritance and variation, the gene, in all organisms derived from them, the original particles possessing them may be described as "naked genes." Their original method of reproduction may have consisted in the accretion of several similar particles simultaneously, but the only system which is known to survive is that where one new particle is formed at a time; the old particle is then said to divide into two. Reproduction in pairs is probably correlated with the universal property of genes that they attract one another in pairs (Haldane, unpublished).

---

* As this goes to press there appears a discussion of certain aspects of this problem by Muller (1932) based on different premises but arriving at similar conclusions in some respects.

The original gene would necessarily be an organic molecule not of the highest order of complexity. It might then change, by mutation, in one or both of two directions: *either* by developing greater complexity in the molecule or by forming patterns of molecules still reproducing as a unit, that is internally, *or* by co-ordinating several qualitatively different, mutated, genes, that is externally. The first of these two types would perhaps have a higher degree of mutability, and is therefore possibly of greater importance in the bacteria and in some fungi.

(ii) **Aggregation and Differentiation.** The second type has evidently been an essential step in the development of all higher organisms. For its development aggregation of genes into groups is required. Aggregation must depend on the development of accessory materials by the genes, to cement them together. Differentiation would necessarily follow in any aggregate from mutation, since the genes would mutate independently. It would have the selection value of permitting greater complexity in the life of the organism. But it would only be preserved by a further property: co-ordination in the reproduction of different genes and their distribution to different daughter organisms. Hence we may say that differentiation demands a primitive form of mitosis, and mitosis may be said to have been promoted by the special selective value of differentiation. Differentiation between genes of the same origin, in the same or different organisms, would arise equally from mutation.

It may be that certain bacteria have never achieved this co-ordination and have remained undifferentiated single-gene organisms. The filterable virus produced by the breaking up of *Bacillus proteus* continues to react with anti-*proteus* serum, *i.e.*, the single element retains the properties of the whole.

The co-ordination of the division of the gene with that of the nucleus (as we must now call the gene-aggregate) might follow if the same conditions determined both or if the one determined the other. It must be assumed that, primarily, division of the genes determined division of the nucleus. (Thus a second division is determined primitively in meiosis.) But in the light of behaviour in the prophase of meiosis of the special phenomenon of polymitosis, it must also be assumed that secondary conditions may lead to division of the nucleus forestalling that of the genes.

(iii) **Construction of Chromosomes.** The distribution of separate daughter genes in a bipolar division of the nucleus would no longer be practicable when a certain volume/area relation was reached, depending on the volume of accessory materials in the nucleus, *i.e.*, the degree of dispersion of the genes in the resting stage. The next step must therefore be the mechanical association of the genes during their separation at mitosis. The following conditions would have to be observed :—

1. An association would produce two similar associations by reproduction of its genes. These two must pass to opposite poles as units. They must therefore have a dynamic centre—a second type of co-ordination. This centre is the spindle attachment. The behaviour of this organ must determine not only the occurrence of separation but the time of its occurrence. This it would do by an internal change probably of the nature of division. Its division would not necessarily synchronise with that of the genes but might well follow it.

2. The symmetrical division into two halves might conceivably be achieved if the association were either *superficial* or *linear*. Superficial association would offer increasing resistance as separation of the two layers proceeded. Even if feasible it would therefore be

less satisfactory than linear arrangement, and for the same reason branched arrangement would be less satisfactory than a simple linear one. A circular structure would give interlocking of its two halves whenever its reproduction was not in the same plane throughout. (Other conditions fatal to a branched or circular structure arise later from the assumption of spiral form and behaviour at meiosis.)

3. The linear association might be haphazard at each mitosis, but that co-ordination with spindle attachments would then be impossible. It must therefore be constant, and the constancy could only be determined by permanent association of the genes, since otherwise it would have to be determined anew at each mitosis by a specific attraction of every gene for the one on either side of it, except the end genes which would have only one attraction. Not only is such specificity incompatible with the genes having any specific properties adapted to their hereditary functions, but it also does not permit of any reduplication of genes in the nucleus, and this restricts variation. The arrangement must therefore be potentially permanent, and its permanence determined by accessory materials themselves controlled by the genotype. Hence the original organisation must have taken place suddenly and probably by the formation of a single chromosome.

4. The formation of a chromosome would only permit of a slight increase in the number of genes so long as the thread remained stretched to its full length at the time of mitosis. With any further increase the difficulties seen in the *Aggregata* sporozoite would become a serious obstacle to regularity. Linear contraction during division would therefore become necessary. To be regular in distribution this contraction must be controlled from one point such as the spindle attachment. The means by which this could take effect would be the assumption of a spiral produced by a state of torsion between the spindle attachment and the chromosome envelope (Ch. X).

(iv) **Spindle Mechanism.** At the earliest stage it is evident that a mechanism external to the genes themselves must be developed to co-ordinate their division. It has now been made clear, from experimental evidence, how far such division can be autonomous in living forms; the development of the spindle must therefore have been auxiliary to this division. It is clear, too, from the experimental evidence described that the spindle is subject to genetic control. It will also be clear from the variations observed naturally in the spindle mechanism—the intranuclear spindle, the lateral spindle found in lower organisms where the spindle is developed to one side of the nucleus, and so on—that the spindle is subject to independent genetic adaptation. This is particularly important in considering later stages of development.

(v) **Structural Change.** If one spindle attachment can be originally developed, new chromosomes can equally be supposed to develop new spindle attachments (as observed experimentally in *Tradescantia* and *Crepis*). When, therefore, fragmentation of the original chromosome occurred, either through external or internal accident of a mechanical kind or through gene mutation at the point affected, the new fragment would have a chance of independent existence. At this point we have the origin of the haploid chromosome " complement " made up of several chromosomes. This haploid complement, being derived from reduplication and mutation of one original gene, would not consist of n genes of n different types ; on the contrary, certain genes would only be represented once, while others would appear two, three or more times. Pairing at meiosis in haploids suggests that all haploid complements still retain this characteristic.

The particular circumstances favouring structural change are, however, to be sought in abnormalities of mitosis of the kind that is going to be considered next.

3. THE ORIGIN OF THE SEXUAL CYCLE

(i) **Fusion or Addition : Diploidy.** Two organisms at the stage of organisation now arrived at might be led to fuse either by accident or by a genetic reaction produced by mutation. The second cause would be more important in evolution, for it would lead to repetition of the process. If the organisms were closely related, the product of fusion would have two sets of chromosomes with similar arrangement of similar genes.

(ii) **Origin of Meiosis.** In the preceding haploid stage of organisation the division of the chromosomes might take place either during the resting stage or during prophase. But in the latter case the attraction of identical genes in pairs before their division at prophase would lead to the pairing of identical genes and possibly result in crossing-over, and hence in structural change. It is not improbable, therefore, that such delay of division or hastening of prophase might occur in the haploid as a genetic or environmental abnormality and have important results. But in the diploid, if this abnormality occurred, it would result in the pairing of all the chromosomes to give the condition known as pachytene, the first step in a meiotic division. Then the delayed division of the chromosomes would take place, and the conditions produced by this would be quite novel. For threads would be produced of half the thickness of those from which they were derived; they would be produced at a time when the chromosomes are in a state of torsion during the assumption of spiral structure; and finally they would be produced at a time when different chromosomes were lying in intimate contact. It is therefore proper to suppose that breakage and reunion might occur between the paired threads at this moment. It also follows from general principles that the four threads formed by division would fall apart in pairs as soon as division is complete, and that these pairs would be the ones within the same original envelope, *i.e.*, from the same parent chromosome. Thus the delayed division of the chromosomes would lead first to their pairing, secondly to their crossing-over and to chiasma formation between them. Chiasma formation may at present be regarded as normally inherent in the pachytene condition. The chiasmata formed would hold the pairs of chromosomes together until anaphase separated them. Owing to the spindle attachments not having divided, pairs of chromatids would act as units at this stage. The daughter-nuclei containing divided chromosomes would divide at once again if, as seems possible, chromosome division cannot occur without determining nuclear division (the second meiotic division). Hence four nuclei would be formed with the haploid number of chromosomes and the sexual cycle would be complete.

Here we may pause to notice a very remarkable fact. If the pachytene condition persisted without division of the chromosomes, to metaphase (*i.e.*, if the prophase were a little more precocious), reduction would automatically occur in a single division. This simple mechanism has never been developed (unless we consider the third division in "brachymeiosis" to be of this kind). Yet it is difficult to believe that there could be any physiological obstacle to a so much simpler modification of mitosis than that which has actually arisen. Indeed, the occurrence of polymitosis shows that there is not. The fact that meiosis takes the complicated course it does and has maintained with uniformity, in nearly all sexual plants and animals, the essential characteristics of this course, depends on one advantage: this system alone provides the conditions of crossing-over without which recombination of genes and secondary structural changes within the chromosome would be excluded. These are the means of securing changes of proportion. The advantage of the new system is that while mutation is a try with new and untested materials (usually a bad try, as shown by *Drosophila*), change of proportion is a try with old and tested materials (often a good try, as shown by *Œnothera*). In the pre-sexual stage of evolution, change is almost entirely restricted to mutation. A lower degree of stability must then be an asset. Such a condition is found in bacteria and seems to have survived in many fungi. In sexual organisms, on the other hand, effective change must largely be by change in proportion, mutation need not be so frequent and greater stability of gene structure is desirable.

The opportunity of recombination is therefore the essential advantage of meiosis. But it is an advantage that is restricted to hybrids, *i.e.*, to organisms in which the genes of the pairing chromosomes differ in quality or arrangement. It follows that meiosis has no virtue except in hybridity. Hence the countless physiological and mechanical devices which have been developed to promote hybridity wherever meiosis occurs. It may also be remarked parenthetically that hybridity has no virtue except through meiosis. An inherent physiological value in the heterozygous condition, *i.e.*, presence of allelomorphic genes in the same chromosome, can be discounted on two grounds, other than experimental: first, since the different genes of any set arose by the same process as allelomorphs, heterozygosis has a mechanical but no physiological significance; secondly, since genes occur reduplicated probably within all haploid sets, the same proportions may be attained between genes and their allelomorphs in a homozygote as in a heterozygote, and, furthermore, such proportions can be selected more efficiently in a homozygote than by the aid of random crossing. It is of course evident that in special instances, where by regular crossing the species has become adapted to it, a heterozygous condition is often advantageous.*

Whether meiosis arose as a new mutation in a diploid, or was already conditioned in the haploid, the resulting cycle would be the same : the first division after fusion would take the form of meiosis, and, in the haploid produced, a series of effectively normal mitoses would occur. (They would not have the character of meiosis in haploids, for the special meiotic spindle mechanism would not have been developed.) The sexual cycle would therefore be of the *Aggregata* type, still found in most of the lower organisms (Fig. 107).

This mechanism, for all its advantage, would obviously be very imperfect, and there are two directions in which it would be developed, and rapidly developed, for the very irregularities arising from its imperfection would provide the genetic material for adaptation, and evolution would take on a new *tempo*.

(iii) Restriction of Meiosis in Time and Space. The original modification of mitosis would apply to all mitoses in the organism. There is no reason to suppose that such a new mutation would have a differential effect on successive mitoses. This would lead to immediate reduction in all diploid nuclei, but would not interfere seriously with mitosis in haploid nuclei. A preliminary to any special improvements must have been the restriction of meiotic conditions by a differentiation in the properties of nucleus at division ; this would be a restriction in time, in unicellular organisms, and in space as well, in multicellular organisms. The restriction would enable the haploid generation derived from it to enjoy complete mitotic regularity and avoid occasional pairing of reduplicated genes ; without such a restriction variation by changes in proportion would be impossible.

---

* The essential part of this argument was understood by Weismann so far as the then state of knowledge allowed, as the following passage shows (1892) : " Da nun die Reduction nicht immer in derselben Weise erfolgt, vielmehr bald diese, bald jene Idanten die Hälften bilden, welche den einzelnen Keimzellen zufallen, so bietet sich dadurch die Möglichkeit, dass die Keimzellen ein und desselben Individuums doch ganz verschiedene Combinationen von Idanten enthalten. Die Folge davon ist die Ungleichheit der Kinder eines Elternpaares, oder allgemeiner : die ungeheure Mannigfaltigkeit der Mischung individueller Unterschiede."

Without such a restriction, moreover, *meiosis must follow fertilisation immediately*, and a series of diploid divisions giving a diploid generation could never arise. The conclusion of systematists that the absence of the diploid generation is the primitive condition in Algæ, Fungi and Protista, is in conformity with this view. In these the time-restriction of meiosis has not been developed and its place-restriction is determined by the restriction on fertilisation.

A state of physiological diploidy could be maintained if the two haploid nuclei were to keep separate and divide side by side in each cell, delaying the final fusion until meiosis was required. The fact that such a mechanism obtains in the " diplophase " of the basidiomycetes, where meiosis promptly follows fusion, suggests that this is the only way in which diploidy can be achieved in this group, on account of meiosis being an inherent property of all their diploid nuclei. By this device the benefits of diploidy have been acquired without the physiological distinction arising between mitosis and meiosis by the restriction of meiosis to one stage of the life cycle.

(iv) Development of the Meiotic Spindle-Mechanism. A specialised property of spindle-development co-ordinated with meiosis would protect the new mechanism from irregularities that would otherwise result both from unlikeness of the pairing chromosomes (hybridity) and from abnormal external conditions. It is from failure of this special co-ordination at meiosis in certain experimental observations that the independence of the spindle from division of the chromosomes in both mitosis and meiosis, and the different character of the spindle mechanism developed at meiosis in different organisms, can be inferred. For example, where pairing of chromosome fails, we see in the Lepidoptera the double division of the spindle mechanism imposes itself regularly on the chromosomes, while in the higher plants it is usually unable to do so. Again, in haploid plants, we see that in one case the spindle is abortive, in another it is able to control separately all the scattered chromosomes and yield numerous separate cells. And considering normal meiosis comparatively we see that sometimes the second division follows immediately, and sometimes it is delayed. All these instances show that a mechanism has arisen distinct from that simple mitotic spindle which must have controlled the first meiosis. Further special instances must be considered later in their special connections.

(v) **Modifications of Chromosome Behaviour.** A great variety of modifications of chromosome behaviour have been developed, presumably as adaptations. The most general of these can be shown to be determined as genetic characters. These are the modifications in the frequency, distribution and movement of chiasmata. It seems that originally, just as now almost universally, the formation of one chiasma was a *sine qua non* of the maintenance of chromosome pairing from pachytene to metaphase, and the formation of a minimum number of chiasmata of one is advantageous. It is also evident that the occurrence of numerous cross-overs in each chromosome at different points in the chromatid in different nuclei is advantageous inasmuch as it gives the greatest variety of recombinations of differences among the gametes. On the other hand, a large number of chiasmata must be mechanically disadvantageous, for it leads to difficulty in the separation of chromosomes unless the number is reduced before anaphase. These different factors of natural selection are best balanced by a random distribution of chiasmata modified by interference, for in this way a low mean number is compatible with regular formation of a minimum of one. Such a condition may be inherent in chiasma formation, but it is equally clear that it may be developed as an adaptation, since races of the same species occur with different degrees of interference.

Two other mechanisms have been developed by which chromosomes can separate with great regularity irrespective of the number of chiasmata in the different bivalents. The first is *localisation* of chiasmata in the neighbourhood of the spindle attachment, which gives a maximum but uniform resistance to separation. The second and more efficient device is *terminalisation*. It seems to be determined by the shifting back in the cycle of meiotic changes of the repulsion between spindle attachments, which normally reaches its zenith at anaphase, to diplotene. It is therefore analogous to the changes in time of action of genes noticed by Haldane (1932 *a*). The movement of chiasmata to the ends of the chromosomes gives a uniform minimum resistance to separation. Terminalisation is, moreover, indispensable for the working of a ring mechanism as in *Œnothera*, for the repulsion of successive chromosomes in a multiple ring only acts efficiently where their association is by terminal chiasmata. Interstitial chiasmata are too rigid to permit of free orientation in the ring, hence a high proportion of non-disjunction and sterility is observed in *Pisum*. Both localisation and terminalisation are clearly genetic properties developed by adaptation, since related pure forms differ in regard to them. Localisation is obviously to be regarded as a *pis aller*, and it is interesting to notice that it is developed in two groups, the Acrididæ and the Liliaceæ, showing the least terminalisation. Localisation is of further interest in that it permits the survival of fragment chromosomes so that the conditions of structural change within the complement are made easier. This is observed especially in the South American Acrididæ. The same result may be achieved by a differential frequency of chiasmata in relation to chromosome length of such a kind that a minimum of one chiasma is formed on each bivalent however short, as seen in *Stenobothrus* and *Hyacinthus amethystinus*.

4. THE DEVELOPMENT OF THE SEXUAL CYCLE

(i) Origin of Sexual Differentiation. With the occurrence of a repeated cycle of sexual processes, differentiation of the fusing cells becomes convenient. This differentiation, as opposed to lack of differentiation, is always a genetic property. The property may condition a different reaction of two haploid cells to different environments. This we see in its minimum development in *Actinophrys*, where opposite cells, differing only in position in the organism, go through meiosis at different rates and the one that is mature first takes the initiative in fertilisation (Ch. I). It may also arise within a multicellular organism, which is then said to be hermaphrodite, and the differentiation may then occur either in space or in time. And finally it may arise between different organisms with similar genetic properties subject to different external conditions. The genetic basis of such differentiation is simple, and not in any way distinct from that concerned with other types of differentiation within and between genetically similar organisms.

Where, on the other hand, sexual differentiation is decided by a genetic difference either between the haploid cells so differentiated or between the diploid organisms which have borne them, as is necessarily the case where the haploid generation is physiologically subordinate to the diploid, the problem is a different one. Such genetic differentiation could arise either in an organism with undifferentiated germ-cells or in an hermaphrodite organism. In either case it demands, for perfection, changes in both the opposed types. If an organism with undifferentiated gametes is to give rise to one with some gametes specialised for female functions and others for male, the differentiation depends on changes in both. If an hermaphrodite is to give new diploid offspring with capacities for producing opposite germ-cells, it must also change in two directions. How is this to be brought about ? Clearly in the first case of haploid differentiation the diploid which is to produce the two kinds of haploid must be heterozygous. In the second case of diploid differentiation one of the two kinds of diploid must be heterozygous, since they differ genetically and yet each contains a chromosome set derived from the other. Such differences cannot develop from a single mutation ; they require at least two to be effective. Moreover, perfection in any genetic mechanism is only possible on a basis of an indefinitely large number of mutations. In the first instance, therefore, rudimentary sexual differentiation must coexist with lack of differentiation or with hermaphroditism. The problem, therefore, is simply one of how a system can be kept in a heterozygous condition permanently, that is, from generation to generation. This can be done in one way only : by the suppression of crossing-over between the affected differences. Structural hybridity might have determined this suppression, but it is unlikely that the structural differences would in the first instance occur in convenient association with the critical gene-differences. It is, on the other hand, easy to suppose that crossing-over was suppressed in the parts of the chromosomes concerned at meiosis in the sex-heterozygote, since factors suppressing crossing-over have been found in experiment, and species with localised chiasmata have been recorded cytologically. Moreover, Haldane's rule that crossing-over is reduced not merely in the sex-differential chromosomes (*X* and *Y*), but throughout the chromosomes in the heterozygous sex in animals, agrees with this view ; such factors act on the whole complement. The restriction of crossing-over must therefore be genotypic in the first instance. Secondarily to this general suppression or localisation of crossing-over, differential condensation, and prevention of pairing of the *X* and *Y* chromosomes themselves, probably arose. Such an adaptation would have the value that the autosomes would enjoy the advantages of crossing-over in both sexes.

It should be noted that systems of sex-differentiation in all living organisms owe their remarkable similarity to the uniform operation of these limiting mechanical conditions (as well as of other biochemical conditions), and not, as is often implied, to a common origin of the systems themselves.

(ii) **Cytological Development of Differentiation.** The exclusion of certain corresponding parts of the *X* and *Y* chromosomes from crossing-over will mean that they will evolve as independently of one another as the chromosomes of two different species, provided that they fulfil their special and relative physiological functions satisfactorily. This means, first, that they will gradually lose all qualitative relationship—a process which is shown by the stages observed in the reduction of pairing at meiosis in different species—and, secondly, that they will lose all quantitative relationship ; the *Y* will be larger or smaller than the *X* according to the convenience of the change ; but being a less efficient agent of evolution, as will be seen later, it will have less value and will consequently, as a rule, be smaller. The qualitative and quantitative differentiation of the sex chromosomes have been observed in every stage of development, from their behaviour at prophase, and relative size at metaphase, of meiosis. They are associated with structural changes of all kinds.

The partial or total exclusion of the *Y* chromosome from intercourse, with the *X* is observed, cytologically, in the differential precocity of the sex chromosomes and their failure of pairing at prophase, and, genetically, in the failure of crossing-over between them. It will have important secondary genetic effects.

The *Y* chromosome will be excluded from the possibility of evolutionarily effective variation for the following reasons: First, since the hereditary properties of the organism depend on the interactions of its constituent genes, variations within a chromosome can only be tested in their most advantageous combinations when they are freely distributed by crossing-over. Secondly, in the absence of crossing-over all possibilities of secondary structural change within the chromosome are excluded, and possibly primary structural change also (since it must be favoured by abnormalities in pachytene pairing). The rate of variation will therefore be reduced. Thirdly, since the *Y* chromosome does not reproduce itself in the homozygous condition it is prevented from elimination through the lethal effect of any recessive characters (*cf.* Muller, 1918, p. 483). These special conditions will mean that the *Y* chromosome will gradually lose its relationship with sex determination, and with the *X* chromosome, and that the autosomes will take up its function. This will occur as a matter of course and without any change of principle on the basis of the theory of qualitative differentiation, for the two sexes from the beginning differ in *X*/autosome proportion as well as in *X*/*Y* proportion.

Any change arising in the autosomes and favouring the heterozygous sex (and such a mutation has been found in *Drosophila simulans*) will be useful as a factor heightening the genetic difference between the sexes. The autosomes will therefore become the effective vehicles of sex-variation, while the *Y* chromosome will lapse into unimportance and a neutral reaction will be favoured. The change produced may be represented in the genetic terminology of Goldschmidt by saying that the factor determining femaleness (in the heterozygous sex in moths) is in the *Y* chromosome in *Lymantria*, but in an autosome in *Abraxas*. Thus the occurrence of differences between different races of *Lymantria dispar* in factors determining sex both in *X* chromosomes and in autosomes shows how the evolutionary change might come about to give rise to the condition of *X*/autosome balance found in *Drosophila*. It is, moreover, precisely in those organisms in which the *Y* chromosome influences sex determination and still crosses over with the *X* that the sex determination mechanism seems to be least permanently established (as shown by the occurrence of related forms without sex differentiation as in the higher plants, or with an opposite sex mechanism as in fishes).

Comparison of sex-chromosome relationships as shown by the relative form of X and Y and the kind and duration of association at meiosis shows the transition expected. In form we have the whole range from apparent identity to the complete disappearance of the Y. In behaviour we have the whole range from apparently normal pairing throughout prophase until metaphase to that at which the chromosomes do not pair at all until the second division.

Reviewing these conclusions in relation to earlier steps, we see that there are broadly three kinds of condition under which genes work and beget themselves: *pre-sexual* in bacteria, *sexual* in autosomes and X chromosomes, and *sub-sexual* in the Y chromosome. The first favours high mutability, the second, low mutability, the third, no mutability, inactivation, or neutrality. The Y chromosome is pre-sexual in itself, but on account of its coexistence with sexual chromosomes any kind of instability becomes a drawback to the functions of its more important fellows, to whose success it is subordinated. In the end, it becomes merely an instrument for securing the regular segregation of the X chromosome at meiosis in the heterozygote.

(iii) **Changes in Sexual Differentiation.** The fact that the evolution of systems of sexual differentiation is seen in all stages of development at the present time must be due to their having been produced anew, or, at least, reorganised, very frequently. More direct evidence of this is found in the opposite systems of sex differentiation seen in related groups such as mammals and birds, or different species of fishes, the one group having heterozygous males (*Lebistes*), the other heterozygous females (*Aplocheilus*). It is also found in the occurrence of genetically unrelated systems of sex differentiation in the angiosperms and in the bryophytes.

There are two possible means by which this change could occur; according to both of these, the new sexes are derived from the homozygous sex of the old species. The first way would be that factor-differences could arise in the autosomes which in the homozygous condition would turn the normally homozygous sex into the heterozygous one. Such sex-reversed individuals have been found in *Lymantria dispar*. These individuals, mated with heterozygous ones, would give both sexes according to the new system of sex determination. It will be noted that primitive sex differentiation from an hermaphrodite or undifferentiated form could not arise from a single factor, but secondary differentiation might.

The second way would be that the homozygous sex could become hermaphrodite, as in *Rana* (Witschi, 1928), and from the hermaphrodite by gradual genetic adaptation a new form of sex differentiation could arise, as it did primitively. This second method is particularly important in considering the origin of the haplo-diploid system of sex differentiation.

(iv) The Haplo-Diploid System. According to this system of sex differentiation, found in Rotifera, Acarina, Thysanoptera, Hymenoptera and two families of Hemiptera, the unfertilised eggs of sexual females develop into (haploid) males and the fertilised eggs into (diploid) females. Numerous attempts have been made to understand the genetic principles of this system by relating it to the ordinary XX-XY type, and assuming some kind of differential balance. These have all proved fruitless, and they might be expected to do so for several reasons.

Thus the new haploid male, arising necessarily in this case from an XX female, would have to compete successfully with the old heterozygous XY male. It is inconceivable that a new " mutation " hampered by irregular meiosis should compete successfully with a type gradually developed by adaptation, especially since the new type would introduce no new genetic advantage (such as the encouragement of crossing). It is still more inconceivable that the new haploid type should have the same sex-function as the differentially balanced heterozygous male, *i.e.*, that $A + X$ should be comparable to $(A + X) + (A + Y)$. The only experimental evidence directly contradicts such a presumption ; haploid patches in a diploid female *Drosophila* are still female (Bridges, 1925).

The first objection does not hold if it is assumed that the new type arose from an obligatorily parthenogenetic species (with no males), but the second objection does hold. Moreover, it is extremely difficult to suppose that such a species—which must usually be regarded as an evolutionary *cul-de-sac* on account of its restricted capacity for variation—should recover the property of normal reduction, and, not being homozygous, produce viable haploids of any kind. If, on the other hand, it is supposed that the haplo-diploid system arose from the gradual elimination of one set, as the Schraders have plausibly suggested (*v*. Ch. XIII), a new principle is involved, for determination becomes quantitative as soon as the second set disappears.

Another method of evolution unrelated to the alternative system is, however, conceivable both mechanically and physiologically. The new system can be supposed to have arisen from an hermaphrodite species. Such forms, owing to deficiency of sperm, sometimes fail to secure fertilisation of all their eggs. In these circumstances haploid individuals that were capable of development would be likely to show differential growth of the sex organs, especially if development in the hermaphrodite diploid were analogous to that in the consecutive hermaphrodites, such as *Rana esculenta* (Witschi, 1928) and many molluscs, or if its conditions were similar to those assumed by Goldschmidt to determine the growth of sex organs differentially with respect to time. With such a genetic background the lowered *tempo* of development characteristic of new haploids would have a differential effect on the development of the sex organs, so that the new haploid would be effectively or predominantly of one sex—the one which was earliest in development. Evidence that such a differential effect can occur is shown by the different proportions in size and number of organs in polyploid series of plants produced experimentally, particularly by the characteristic differences of habit between haploids, by the different production of vitamin D in diploid and triploid apples (Crane and Zilva, 1931), and, most significantly, by different relative time of appearance of opposite sex organs in diploid and tetraploid *Bryum* (v. Wettstein, 1924). These observations show, in a word, that quantity as well as proportion may have a differential effect. Schrader and Sturtevant, in their hypothesis that sex was determined by the algebraic sum of opposite determinants, tried to show that it might be quantity *instead of* proportion that had the differential effect in this system and in the *XX–XY* system, and thus put the two types of sex determination on the same footing, a position which is untenable on the evolutionary and genetic grounds given above. A differential effect, although unnoticeable in the sex differentiation of an organism where its reaction was well on one side of the threshold value (as in female *Drosophila*), might nevertheless have a critical effect on an hermaphrodite in which the factors affecting the development of opposite gonads must be balanced and their effect therefore labile.

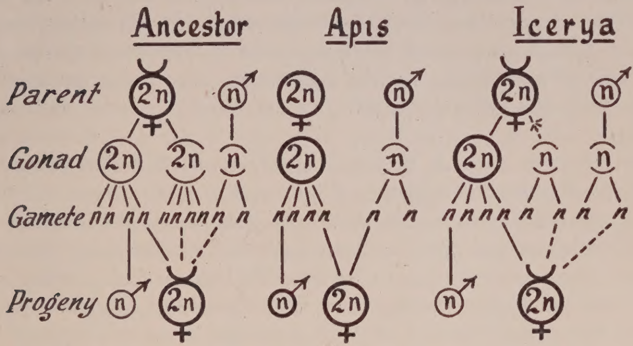


FIG. 108.—Scheme of reproduction in an imaginary ancestral type with optional haplo-diploid sex-differentiation, in the normal haplo-diploid type (*Apis*), and in a derived type *Icerya*.

The result may then be represented as due to a shortening in the time of development of an organism with differential rates of production of opposite sex stimulants at different times whose normal equilibrium gives an hermaphrodite. A corresponding differential rate of development of opposite sex glands has been found in *Perla marginata*. In the male larva, attached to the testis, ovarian tissue is found which later disappears (Junker, 1923).

Let us first suppose that the new haploid is predominantly male. Its germ-cell formation will be irregular, but some functional sperm will be formed. The position then will be that the hermaphrodite type will normally produce a proportion of haploid males or sub-males and crossing with these will co-exist with self-fertilisation or crossing between hermaphrodites. Now the crossing with males will have a special value in competition with a system permitting selfing. In this regard it should be noted that the chief means of obtaining obligatory crossing in hermaphrodite animals—by alternation of sex in the individual—is impossible in the insects, where sexual maturity brings development to an end. Any mutation therefore favouring the new system would have genetic value. This would be achieved by (*a*) greater femaleness of the hermaphrodite type, (*b*) greater maleness of the haploid type, and (*c*) modification of meiosis in the male to give regular failure of reduction. For the first two changes any mutation exaggerating the original genetical effect would serve (and all genetic differences are subject to genetic exaggeration) ; for the last change, a modification of the spindle in different ways would give the effects found in *Apis* and *Icerya*.

At an early stage an optional condition very like that found in *Icerya* would arise. There, 1 per cent. of the eggs of the hermaphrodite are unfertilised and give males ; the rest are self- or cross-fertilised and give females. From the evolutionary point of view *Icerya* is, however, to be regarded, not as representing an intermediate type, but rather as derived from a simple haplo-diploid type by the insertion of a haploid male stage in the development of the female, but its behaviour is important in showing that functional hermaphroditism and haploid maleness can exist side by side. At a later stage the new system, favoured by natural selection owing to its obligatory cross-fertilisation, would gradually displace the old (Fig. 108).

Now, on the other hand, the new haploid might be predominantly female, and this on physiological grounds is equally probable. But such an innovation could never survive, for obvious reasons : the haploids would arise through lack of sperm and would increase the very shortage to which they owed their origin, while the diploids could never cease to be female, as well as male, if haploids were to be produced. The haploid-male innovation, on the other hand, on the present hypothesis, would remedy the error to which it owed its origin, and every step in its improvement would necessarily mean an increase in the fertility of the species.

5. THE STABILISATION OF HYBRIDITY

(i) The Development of Apomixis. Experiment and comparison show that hybridity and the inheritance of special genetic properties may in certain instances independently determine the occurrence of apomixis. The problem of apomixis is the problem of the part these two properties play in its origin.

In the first place, it is clear that special genetic properties are necessary, permitting the development of unfertilised eggs, pseudogamously or otherwise, for parthenogenesis, and permitting the development of adventitious embryos in the absence of successful sexual embryos, for apospory and nucellar embryony. These properties are probably characteristic of certain genera such as *Hieracium* and *Aphis*. Secondly, it is necessary that unreduced eggs should be produced, for diploid parthenogenesis, and unsuccessfully reduced eggs, for apospory. It is this second property that needs special consideration.

For this purpose it is important to distinguish between hybridity and a genetic property more clearly than has been done in the past. Hybridity has no universal significance except in regard to effect on meiosis. It has therefore been defined as the property of a zygote having arisen from the union of gametes dissimilar in respect of their chromosomes (Ch. V). This dissimilarity is first felt when the chromosomes come together at the pachytene stage of meiosis. It is equally effective in destroying the regularity of meiosis in a numerical hybrid, where the dissimilarity consists merely in a difference in the numbers of chromosomes, and the chromosomes of each type are exactly identical (*e.g.*, in auto-triploids) and where it consists in particular differences between corresponding chromosomes (*e.g.*, in a diploid interspecific hybrid). In a word, hybridity must not be considered in a taxonomic or phylogenetic sense.

In a hybrid their dissimilarities prevent the chromosomes coming together at pachytene, although we are not usually able to show this cytologically except by inference from the later behaviour. Now this property depends entirely on the relationship of the two chromosomes. But precisely the same result can be obtained, not through dissimilarity, but through the hereditary properties of the individual. In *Rhabditis* pairing of chromosomes fails, although they are known to be identical, and this has been shown to be an hereditary property, *i.e.*, a property of the germ-plasm as a whole, and not of the relationships of its parts.

Viewed in this light, all apomixis can be seen to be primarily conditioned by the hereditary properties of the individual which makes development possible without fertilisation. Further, it can be seen that the development of this hereditary property is in many cases independent of hybridity. This is most obvious: (i) in organisms that are cyclically or facultatively parthenogenetic (Aphides, Rotifera, Cladocera, *Apotettix* and *Paratettix*, *Allium*, etc.); (ii) in others in which parthenogenesis is a means of sex determination (Hymenoptera, Rotifera); (iii) in many pseudogamous plants with good pollen (*Zephyranthes*, *Potentilla*); and (iv) in animals and plants in which the pairing of the chromosomes is perfect (*Rhabditis*, *Solenobia triquetrella*), especially those which are facultatively sexual and true breeding (*Elatostema sessile*, *Thalictrum purpurascens*, *Allium odorum*). Robertson, in his argument (1931) that some of these cases can be attributed to hybridity *per se*, fails to distinguish consistently between this and specific genetic factors segregated in the progeny of a hybrid, and his conclusion is invalid. Thus, in all these examples, parthenogenesis is compatible with complete homozygosity.

There is a second class in which the decisive influence of hybridity can be seen: in those aposporous plants which are facultatively sexual but not true breeding. Apospory, in itself, is no more obscure than such teratological observations as those of Stow (1930), who induced the formation of a structure in the pollen grain of *Hyacinthus* resembling the female gametophyte. That such abnormal structures should be able to function is evidently conditioned by sexual failure. Lidforss's experiments show that the lack of viability of the sexual embryo stimulates apospory. In such forms apospory must be conditioned by partial sexual sterility which itself is sufficiently accounted for by either hybridity or cross-fertilisation.

It is probably of no account whether or not sexual failure is determined by interspecific hybridity. Irregularity of meiosis is as characteristic of non-hybrid tetraploids as of hybrid diploids, and tetraploidy of this kind is probably a determining factor in some species, *e.g.*, *Nigritella nigra*, which exists in a diploid sexual form ($n = 19$) and a tetraploid apomictic form, with nucellar embryony (Afzelius, 1928; Chiarugi, 1929). In triploids the conclusion to be drawn is unequivocal: the last sexual act in their history was an act of hybridisation, not necessarily between different species but between gametes with different chromosome numbers. If, in these, hybridisation determined the institution of apomixis, in many others where clear-cut evidence is lacking this kind of origin may be readily presumed.

A third class of organisms, with obligatory diploid parthenogenesis and defective chromosome pairing (leading to the suppression of meiosis), presents a more difficult problem. We might equally well suppose, *a priori*, that the observed suppression of meiosis was a genetic property or the result of hybridity. But in species of *Eu-hieracium* (Rosenberg, 1917, 1927) it has been possible to trace stages in the development of the suppression. Applying to these the results of our earlier analysis of aberrations of meiosis (Ch. XIII) it is possible to define the conditions of the development.

In the first stage of "degeneration of the reduction division," *i.e.*, abortion of the first meiotic division, the *Boreale* type, we see the ordinary symptoms of hybridity: pairing at pachytene but not at metaphase; the failure of metaphase pairing is due to the same cause in these hybrids as in the fragments of non-hybrid species, an insufficient length of chromosome paired at pachytene to lead to the formation of a chiasma. But, in the last stage, *Pseudoillyricum*, with suppression even of pachytene pairing and development following a temporary contraction, we have a phenomenon that is not characteristic of hybrids, as such. Clearly a primary condition of meiosis is wanting, and on the precocity theory this might happen in two ways: either (i) the division of the chromosomes is relatively advanced, or (ii) the beginning of prophase is relatively retarded, so that at leptotene the chromosomes are already doubled and therefore have no attraction for one another. That both these aberrations are indeed conditions of various types of abnormality found in meiosis is shown by the time discrepancies observed in several apomictic and sexual genera. The irregular nuclei are either advanced or retarded (Ch. XIII). The mitotic length of the chromosomes at the first division is evidence also of lack of precocity. The special contraction which replaces metaphase is also an abnormality not known in new hybrids and therefore, we must suppose, genetically conditioned. We see then, on purely cytological grounds, that the suppression of meiosis in its simplest form is conditioned by hybridity, in its most advanced form by a genetic property.

Thus three conditions appear to determine diploid parthenogenesis in its most advanced form in the *Eu-hieracia* and elsewhere : (i) A genetic property, particularly common in some genera, conditioning parthenogenetic development of the embryo-sac ; (ii) hybridity conditioning the original formation of unreduced embryo-sacs, as found in the *Pilosella* section ; and (iii) a genetic property acquired later by adaptation, perfecting the mechanism by which suppression takes place and probably consisting in a derangement of the ordinary time relationships of meiosis ; the first stage of this is found in *Boreale*, last stage in *Pseudoillyricum.*

A difficulty arises when we come to consider how this third condition can be attained by adaptation in a parthenogenetic organism. This difficulty has been felt in another connection. Genera of plants in which apomixis is general commonly show a remarkable polymorphism. This is particularly true of *Rubus* and *Eu-hieracium.* And in *Eu-hieracium* Ostenfeld found 60 parthenogenetic species and only three sexual ones (*cf.* Rosenberg, 1917). How has such a remarkable polymorphism arisen in the absence of the two recognised means for the distribution and recombination of variations, *viz.*, meiosis and fertilisation ?

Ostenfeld and many others have sought to explain the phenomenon as the result of mutations (1921). As a rule the progeny of a parthenogenetic plant or animal are as like their parent as conditions permit ; in plants they constitute a " clone " of the same uniformity as one reproduced by cuttings or bulbs. Ostenfeld, however, showed that two " mutations " occurred in 1260 parthenogenetic seedlings of *H. tridentatum.* It is now possible to consider (contrary to the earlier belief) that suppression of meiosis leading to failure of reduction will not lead to failure of segregation when any two chromosomes have paired. When the two chromosomes that have paired separate at the first division, but are included in a single restitution nucleus, their second division, which gives the two

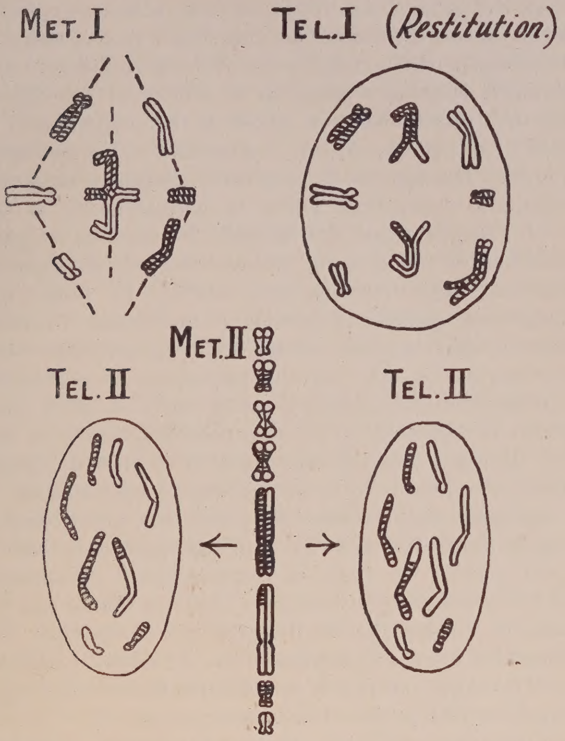


Fig. 109.—Scheme showing how a restitution nucleus will give numerically unreduced gametes showing segregation of differences so long as pairing of dissimilar chromosomes occurs (*cf.* Fig. 105).

unreduced germ-cells, will, on the chiasmatype hypothesis, not be equational. Thus if crossing-over must occur at the chiasma which conditions their pairing, the second division will always be reductional in regard to one of the cross-over segments. In either case the result will be equivalent to mendelian segregation of the differences in the pairs of chromosomes concerned. It follows, therefore, that a hybrid in which a pair of chromosomes is occasionally found at metaphase and in which failure of reduction is due to suppression of the first (or indeed the second) division should show a very limited amount of segregation. Suppression of the first division will give diploid nuclei showing segregation in respect of the differences between such chromosomes as paired in the proportions 1 : 6 : 1 instead of 1 : 2 : 1 (*cf.* D., 1930 *a*). Segregation will be appropriately toned down. This conclusion, on general grounds, is supported by v. Wettstein's observations (1924) of heterozygosity in diploid spores of *Funaria* when the second division was suppressed, and possibly by Harrison's observations of segregation in the parthenogenetic progeny of a moth. In short, diploid parthenogenesis appears to provide a mechanism whereby an organism in which normal meiosis would give sterility through excessive segregation, may show limited segregation and be fertile.

The mechanism is analogous in its effect to that whereby segregation is restricted in the tetraploid derivatives of diploid hybrids. It seems plausible that Ostenfeld's mutants (which he empirically described as " the after-effects of hybridisation ") are really segregates of this kind. Most such segregates being more homozygous should be less fertile than their parent, as these were. They will provide the basis of polymorphism. The mutations inferred in the relatively homozygous *Cladocera* (Banta and Wood, 1928) cannot, of course, be due to segregation of any kind. Nor is the segregation found in parthenogenetic *Apotettix* (*cf.* Robertson, 1931 *a*) of this kind, but merely first division mendelian segregation in an organism with perfect chromosome pairing.

These mutations will also provide the basis of selection for adaptation of the meiotic mechanism to more perfect conditions for parthenogenesis, *i.e.*, for developing the genetic character which is the second step in the evolution of fertile parthenogenesis. Nor should this be difficult. The appearance of factors for the suppression or partial suppression of meiosis in mutants and segregates of sexual species and hybrids is common enough (Ch. XIII). And while in these any such mutation is a disadvantage, in incipiently parthenogenetic organisms, it will have the highest positive selection value.

Conclusion. The following are the chief independent conditions determining habitual apomixis :—

(A) A genetic property of allowing the development of the egg-cell without fertilisation and with or without other stimulus, such as false fertilisation (Lidforss, 1914) or degeneration of neighbouring tissues (Haberlandt, 1921, *a* and *b*). This is not inherent in all living organisms, but is widespread in certain groups of plants and animals, and is probably inherent in those with normally zygotic meiosis.

(B) A genetic property determining the development of other cells than the spore in the embryo-sac or embryo (*cf.* Andersson, 1931) [condition of apospory and nucellar embryony] or of other cells than the egg-cell into the embryo [condition of apogamy]. This effect is usually conditional on failure of the facultatively sexual embryo.

(C) Hybridity in the sense determined by its relationship with meiosis, leading to either (i) failure of numerical reduction and partial suppression of segregation (*cf.* D., 1930 *a*) which with (A) gives diploid parthenogenesis (*cf.* Harrison, 1920), or (ii) sterility through segregation, whether in a mendelian sense or as regards the distribution of whole chromosomes, which with (B) gives apospory (*cf.* Chiarugi and Francini, 1930).

(D) A genetic property determining : (i) fusion of a polar body with the egg nucleus, or of two segmentation nuclei ; or (ii) failure of numerical reduction (*cf.* P. Hertwig, 1920) owing to alteration of the time relationship of meiosis. With (A) this property gives diploid parthenogenesis in many plants and animals. It may be acquired as an adaptation by selection of segregates secondary to (C), which alone is an imperfect basis for diploid parthenogenesis.

(ii) Ring-Formation: The Complex Heterozygote. The association of a chain or ring of more than two chromosomes in a diploid is found in hermaphrodites like *Œnothera*, *Rhœo*, and *Campanula*, and in the sex heterozygotes of organisms like *Humulus japonicus*. In both cases it is due to an interchange of segments between non-homologous chromosomes at some point in the ancestry of the organism, since its common ancestors had simple pairing of similar chromosomes. In both cases it constitutes a permanent system like the other systems that have been discussed. What are the circumstances that determined its survival and adaptive development ? The ring of fourteen chromosomes in *Œnothera* can only have arisen by the preservation of a series of changes, whether these arose directly, by mutation, or indirectly, by hybridisation of mutated homozygotes. Their survival and true-breeding is easily understood for the occurrence of interchange, if due to crossing-over between relatively translocated segments in different chromosomes, would give new chromosome types which would be deficient or reduplicated in the segment concerned and therefore lethal in the homozygous condition. But it is necessary also that the new permanent heterozygote should compete successfully with its homozygous relatives. For this its permanent hybridity combined with regular self-fertilisation seems a sufficient explanation. Again it may be said that the value of the hybridity lies not in heterosis but in the property of mutation and consequent adaptability so characteristic of the heterozygous *Œnothera* species.

The development of this property must depend on a differentiation between the chromosomes of opposite complexes essentially like that between the sex chromosomes.

(iii) **Polyploidy.** The importance of polyploidy seems to depend on precisely the same factor as that of ring-formation, *viz.*, adaptability. The polyploid can and does vary in two ways not open to its diploid ancestor. First, it can show a restricted " secondary " segregation of the characters of the parental species. This segregation, like that assumed to occur at an early stage of diploid parthenogenesis in hybrids, will be toned down to an appropriate level, for the more dissimilar the species the more rarely will their chromosomes pair and segregate. Secondly, it can change by change of balance. A tetraploid can give hexasomic progeny having only the slight degree of unbalance found in a trisomic diploid, but unlike trisomic diploids they will be potentially true-breeding. This accounts for the origin of secondary polyploids, which must usually differ sharply from their primarily balanced ancestors but yet have achieved the change in one step.

The absence of polyploids in some groups is probably due either to the inviability of the first generation, which is necessarily giant, or to its failure to segregate dwarfing factors in a later generation such as will enable it to assume a suitable size ; or, possibly, to its failure to reduce the size of its chromosomes to proportions suitable for the required size of cells, whence, perhaps, the absence of high polyploids in some liliaceous genera. Chromosome mechanics demand a fit proportion between the size of the chromosomes and that of the cell.

Fertile polyploid species are all more or less allopolyploid, *i.e.*, hybrid and mechanically diploid. They may have arrived at the condition in two opposite ways. Either a hybrid diploid has doubled its chromosome number (somatically like *Primula kewensis*, or germinally like *Raphanus-Brassica*) thus giving the allopolyploid directly. Or a non-hybrid diploid has similarly doubled its chromosome number, thus giving an autopolyploid with four identical sets of chromosomes, and these four sets have later become differentiated in successive generations through structural change. Every change of this kind would have a high selection value, for it would reduce the formation of quadrivalents and thus increase fertility. In the origin of most polyploids these two methods have probably been combined : the original form was slightly differentiated and later changes have accentuated this differentiation. But in certain species the latter process alone has probably been effective. These are species where two forms, the one diploid and the other polyploid, occur with little or no systematic difference between them. In these the polyploid can scarcely have arisen from hybridisation ; it must have become a hybrid by internal change. Such changes as translocation and inversion would effectively prevent the pairing of originally similar chromosomes without leading to any change of importance in the phenotype. In these cases it is interesting to notice that polyploidy in permitting the survival of the aberrant strain has achieved an interruption in the development of the species. It exists, not as a valuable adaptation, but as an unavoidable accident. The same is probably true in many instances of obligatory parthenogenesis.

6. CONCLUSIONS

(i) The Sources of Variation. The primary source of variation, as we have seen, is the gene change which may be inferred from genetic experiment and also from the existence of qualitative differentiation between the chromosomes. The secondary source of variation consists in structural and numerical change which alters the proportion in which different genes are present. It is best observed cytologically.

The relative importance of the two sources may be judged similarly on genetic and cytological evidence. While all variation is ultimately derived from gene change, proportion changes are evidently more important as immediate agents of variation. Gene change is usually disadvantageous, while proportion change is often advantageous. The reason for this is clear. Gene change is as random as the chemical constitution of the genes permits, and it is biologically untested. Proportion or quantity change makes use of tested materials and introduces nothing new, rather transposing the key of the melody than changing the individual notes. The importance of proportion change, however, must depend on the frequency of hybridisation ; for while the success of new variants from both sources requires a trial in different combinations, which are procured by hybridisation, proportion changes to a great extent owe their origin to the recombinations that arise at meiosis in hybrids. This, in fact, is the important work of hybridisation in evolution.

Another kind of evidence of the relative importance of gene change and proportion change is provided by the differences that can be inferred cytologically between chromosomes of different degrees of relationship. For example, there are differences between homologous chromosomes of related species, between the differential *X* and *Y* chromosomes in sex heterozygotes, between corresponding chromosomes or pairs of chromosomes in complex heterozygotes and between the corresponding chromosomes of different sets in allopolyploids. Finally, there are the differences between the different chromosomes in the same haploid set, for which we have assumed a common origin of the greatest remoteness. The cytological evidence of these differences consists in observations of shape of the mitotic chromosomes and of the failure of their pairing at meiosis—both evidence of structural change rather than of gene change. It seems to show that structural change is of varying importance as between homologous chromosomes of different species, but is all-important as between the chromosomes that are differentiated within the same complement in complex-heterozygotes, sex-heterozygotes and polyploids. The differences, or rather the likenesses, within the same haploid set are an indication of the relative importance of reduplication which will create likenesses and of gene mutation which will destroy them. Observations on *Œnothera* show that at least in this genus the effects of reduplication are not very rapidly smothered by mutation.

The effects of proportion changes are shown by a third kind of evidence. Secondary polyploidy is purely a proportion change. In several instances it has been the means of a sudden evolutionary step of importance.

Summarising the evidence in the simplest way, we can say that variation arises in three stages: (i) gene mutation, which is a property inherent in gene propagation; (ii) structural or numerical change, which is chiefly conditioned by irregularities of meiosis; and (iii) changes in proportion from "secondary" structural and numerical changes, which are conditioned by hybridisation. These three stages in the arrangement of genes can be represented diagrammatically as follows:—

$$\begin{tikzcd}
\overset{A}{aaaaaaa} \arrow[r, "\text{(i)}"] & \overset{B}{abcdefg} \arrow[r, "\text{(ii)}"] \arrow[d] & \overset{C}{abcgfed} \arrow[dl] \\
& \begin{matrix} abcdefg \\ abcgfed \end{matrix} \arrow[r, "\text{(iii)}"] & \begin{matrix} abcdefed \\ abcgfed \end{matrix}
\end{tikzcd}$$

We see from these various considerations that gene change on the one hand and proportion and quantity change on the other are both essential agents of evolution, but differ in relative importance according to the special conditions. They are, however, both determined in quality by the inherent properties of the genes making up the complement. Gene mutation is a specific property of the gene itself. Proportion variation is limited by the relations of the complement as a whole to its individual constituents.

Thus the direction and amount of evolutionary change can be said to be conditioned by three factors :—

(i) The specific properties of the genes, as a primary factor.

(ii) Internal environment, *i.e.*, the balance of the genes, as determining the reaction of the whole to a change in any one of its parts (a special kind of natural selection).

(iii) External environment as an eliminating factor (natural selection in its original sense).

The first two factors will always be similar in effect in related forms ; when the third factor is similar and the forms are unable, for geographical or physiological reasons, to cross, the resulting evolutionary change will be parallel, and when the change is determined by a change in proportion it can be cumulative. These conditions will therefore account for the internal forces in evolution responsible for Berg's "nomogenesis," and for the evolutionary history described by palæontologists as "orthogenesis."

(ii) The Nature of Species. It has been possible so far to consider evolution with little reference to the existence of species. Species which, before Darwin, were a symbol of fixity, have since become a symbol of evolution. But they are merely the bye-products of evolution depending on a variety of unessential accidents which lead to discontinuity. The variations that distinguish them seem to be all of kinds that are known within species (*cf.* Haldane, 1930). The following table illustrates the close parallelism between the two.

Species are important, to systematist and geneticist alike, in two respects : in their external relations and in their internal relations. In regard to external relations, it is clear that discontinuity between species is due to isolation being followed by independent variation. Isolation is doubtless often brought about by distribution, by change of habit, or by genetic sterility factors ; it is also brought about by structural and numerical changes in the chromosomes, which at the same time determine genetic changes.

In regard to internal relations, plant species are shown by

TABLE 66

Variation within and between Species

Change (naturally occurring).	Between Races.	Between Species.
Gene mutation.	In many species.	In *Primula*, etc.
Polyploidy.	*v.* Table 36.	Most genera of dicotyledons.
Secondary Polyploidy.	*Nicotiana.*	*Dahlia*, Pomoideæ.
Fusion.	*Mermiria*, etc. *Phragmatobia fuliginosa.*	*Stenobothrus* and other Acrididæ.
Fragmentation.	*Vicia Cracca.* *Ranunculus acris.*	*Fritillaria.*
Inversion.	*Drosophila* spp.	*Drosophila.*
Reduplication.	Unequal chromosome pairs in species (Ch. VI).	Unequal chromosome pairs in hybrids.
Loss (deficiency).		
Interchange.	*Datura Stramonium.* *Campanula persicifolia.*	*Datura.* *Œnothera.*
Translocation.	*Pisum, Œnothera.*	*Datura, Drosophila.*
Cytoplasmic differences.	*Linum.*	*Œnothera, Epilobium, Funaria, Geranium.*

their chromosome constitution to have a greater variety than animal species, probably owing to the prevalence of vegetative propagation and of hermaphroditism, which latter both permits and demands a variety of means of stimulating cross-fertilisation or stabilising hybridity.

The simplest kind of plant species is that comprising one diploid type. Its internal character is determined by whether it can cross with related species, by whether it mutates freely, by whether it is largely self-fertilised or obligatorily cross-fertilised, owing to self-sterility. These conditions apply to other types of species, apart from the special conditions that become important in them. Diploid species may also be facultatively apomictic.

The second type is the *polyploid* species. Its internal constitution will depend on the degree of differentiation of its dissimilar chromosome sets. When this is slight it will produce by secondary segregation aberrant types which will contribute to the external heterogeneity of the species.

The third type is the *mixed* species, which comprises several numerically or structurally different forms. When these are polyploid forms, they are intersterile, or give sterile offspring together. When they are structurally different, they are also more or less intersterile. Such sub-species are therefore always potential new species, although they may not be clearly distinguishable, apart from their chromosome constitution.

The fourth type of species is that with a pair or group of chromosomes having a differential effect determining sex. These species sometimes have supernumerary fragments derived from parts of the sex chromosomes. The type differs sharply from the simple diploids not only in its obligatory diœcism and secondary sexual differentiation, but also in the species consisting of two groups of individuals, the one homozygous, the other heterozygous in respect of differences that distinguish them, or haploid. They have affinities, however, with the next type, inasmuch as one sex is a permanent hybrid.

The fifth type is the complex-heterozygote. Its behaviour seems to depend on the degree of differentiation of the two complexes which is least in unstable new forms like *Œnothera Lamarckiana*, and strongest in old and stable forms like *Œ. muricata* and *Rhœo discolor*. It must also depend on the possibilities of crossing which are abundant in *Œnothera* and *Campanula* and absent in *Rhœo*.

The last type of species is what may be described as the clonal species. Such species may reproduce by obligatory apomixis (parthenogenesis or apospory, as in *Hieracium* and *Rubus*) or by purely vegetative reproduction (with bulbs, runners or viviparous bulbils, as in *Tulipa* and *Festuca*) or by " semi-clonal " reproduction (as in the *Caninæ* roses, Ch. XIII). None of these are capable of normal sexual reproduction. They often have odd chromosome sets or supernumerary fragments. They are, in general, therefore characterised by uniformity within the species (or " micro-species ") together with slightness of differences between species, unless elimination has removed intermediate forms.

The description as species of all these different types has been found convenient by the systematist, and clearly systematic convenience is the sole criterion that can as yet be applied universally. Consistency, whether morphological, genetical or cytological, if possible in theory, would be impossible in practice. Rules can, however, be applied to the study of an individual species when its systematic character, method of reproduction and chromosome constitution are known.

(iii) The Principles of Evolutionary Change. Consideration of the evolution of genetic mechanisms is particularly enlightening with regard to the principles of evolution, because many of the decisive steps by which great systems have arisen can be repeated under experimental conditions. It is not a question of waiting for a thousand generations to see how the change from sexuality to hermaphroditism, or from fertilisation to parthenogenesis, from homozygosis to complex heterozygosis, or from diploidy to polyploidy and secondary polyploidy, can be produced. These are all irreversible evolutionary steps, and they can all happen in one generation. Indeed, they must so happen. Meiosis, for example, cannot arise from mitosis by a succession of changes. Any half-change wrecks the whole system. This the most decisive change in evolution, must have taken place by one effective mutation. All changes happen through alterations in the chromosomes which are of two kinds: gene mutation and structural change, the latter leading either merely to changes in the arrangement of the genes or to changes in the proportions in which they are present as well.

Most of these changes arise under conditions that cannot be distinguished from normal conditions. Gene changes can only be related to natural radiation and structural change to the inherent properties of the chromosomes, especially in the way they pair at meiosis. Polyploidy alone can be regarded as a character acquired by the effects of abnormal conditions. But from abnormal temperature the opposite results of haploidy and tetraploidy arise, the former disadvantageous, the latter often advantageous, neither having any relation to the efficient cause of the change. No change has yet been induced in any chromosome mechanism which has any adaptive relation to the circumstances inducing it.

It is therefore clearer in the chromosomes than in any other structures that the hereditary properties always arise in advance of the uses to which they are put. Sexual reproduction is not an adaptation to conditions that preceded it but to conditions that followed it. Evolution proceeds because the new forms and properties that arise by chance occasionally (in the phrase of Lucretius) beget a use. They may not beget any active kind of use. Polyploidy and apomixis permit the survival of sterile hybrids, giving them a new lease of life. But polyploidy, as we have seen, may leave the species just where it was and apomixis cuts it off from the main channel of variation. Again other forms may never beget a use for themselves at all. Such are probably most nucleoli and the micro-chromosomes of many Hemiptera. Finally, all forms survive their use. Such are the pollen in the apomictic plant, and the *Y* chromosome in many animals. In the time scale of evolution form overlaps function at both ends ; it anticipates it and it survives it. All this is clearer in genetic mechanisms than in their physiological products, because the mechanism is less plastic than its own materials which determine physiological variation.

Now the Lamarckian hypothesis assumes that evolution proceeds gradually from the accumulated effect of changes in the body of the organism, adapted to abnormal conditions, in modifying the properties of the germ-cells to give the same changes. This means that the body of the organism has some special reaction to " abnormal " conditions of environment which does not occur in " normal " conditions and which affects the germ-cells in a specific way. The principles of change shown by observations of chromosome behaviour conflict with every assumption in this theory. They show that the important changes do not arise gradually but suddenly. They show that the changes do not arise for the most part under abnormal conditions, but under normal conditions. And finally they show that the changes are never adaptive to the conditions that produced them, but that adaptation arises by selection, most of the original changes having been disadvantageous ones.

The Lamarckian assumptions, which are plausible in explaining the evolution of gross structure, break down in face of observation of genetical mechanisms. On the other hand, the essential Darwinian assumptions, of variation followed by natural selection, hold good. In two directions only they require modification : Variation, as Bateson first maintained, is discontinuous, whether by gene or by structural or numerical change. Variation may be described as random in a Darwinian sense when taking place by structural change, but it is random in a chemical sense, and almost entirely deleterious, when taking place by gene change. Yet from the few gene changes that prove satisfactory all organic variation is derived.

APPENDIX I

CYTOLOGICAL INTERPRETATION

> "Nothing more true than not to trust your senses
> And yet what are your other evidences ? "
>
> BYRON, *Don Juan*, c. xiv.

THE cytologist investigating chromosomes chiefly depends on the observation of fixed and stained material. He has two means of judging the value of particular preparations for his studies. The first is by the inductive-deductive method. The effect of particular reagents and treatments on particular structures is determined, laws of behaviour are induced, and from these the value of any particular treatment deduced. This method has been attempted earlier (by Fischer, Yamaha and others), but it has never yet been practicable because the character of the organisms treated, the methods of treatment, the reagents used, and the objects pursued, are all so very diverse in relation to the amount of comparative study that can be carried out. He therefore has to resort to a second more empirical method as being of more immediate practical importance.

This method is the method of comparison of observations, and it may be applied in three ways :—

(i) The observations may be compared with those of living material of the same organism at the same stage of development. This test has been usefully applied in the resting nucleus (Schaede) in the prophase of meiosis (Pl. VIII) and elsewhere, but it is necessarily of restricted use with the ordinary microscopic technique.

The ultra-violet microscope has increased resolving power and increased selectivity both in regard to focus and absorption. Thus photographs of living cells taken by ultra-violet light have a sharper definition and much sharper contrast at a higher magnification. Chromosomes particularly have a strongly differential absorptive capacity as compared with cytoplasm, not only during mitosis but—and this may prove of the greatest significance in relation to the theory of continuity—also during the resting stage. It has already been possible to take photographs of living cells agreeing with those hitherto taken of fixed and stained cells and in some respects equally instructive (Pl. VIII). This method evidently has an important future, especially perhaps in the study of stages in the chromosome history of organisms which have not proved amenable to observation by the customary methods (Lucas and Stark, 1931).

(ii) The observations may be compared with those of related organisms at the same stage of development (after similar or different treatment). In this way a study of the chromosomes at mitosis and meiosis in material which has satisfied the first kind of test enables us to conclude that such structures as constrictions and chiasmata are present in other material less suitable for study on account of the concomitant conditions found, *e.g.*, an inturned bend in the chromosome at the constriction or a change of plane in a diplotene loop or opening of the chromatids in anaphase at the chiasma. The same criterion has been used to show that multiple ring formation at meiosis is the result of normal development of structurally abnormal chromosomes, in hybrids.

(iii) The observations may be compared with those of the same material at the stages immediately preceding and following. This method is essential in the interpretation of meiosis in regard to the pairing of the chromosomes, the movements of chiasmata, the separation at anaphase, the frequency of association, and so forth, and, in examining these, quantitative methods are often necessary. Developmental comparison has shown, amongst other things, the invalidity of the theory of telosynapsis (Ch. XI). Developmental comparison is equally essential for many minor inferences. For example, nucleolar material surviving to metaphase at meiosis in many forms may be mistaken for free small chromosomes produced by fragmentation unless different stages are compared critically.

It is not yet possible to show the whole course of meiosis in all organisms on account of two major difficulties : (i) The occurrence of stages when the chromosomes are collapsed to one side of the nucleus ; this is usually at zygotene and diplotene, probably for the reason that the chromosomes at these stages are slenderer than at the stages between them and following them, so that sudden dehydration leads to extreme distortion. (ii) The occurrence of a diffuse stage when, as though in a resting stage, the chromosomes are lost to sight. Either of these interruptions is fatal to the study of the succession of stages, and all three may occur in the same species (Chick, 1927, on *Benacus*). These difficulties make the comparative method even more important in studying meiosis.

Similarly, the method of division of bivalent chromosomes shows the relationship of the spiral structure to their constituent chromatids (Chs. II and IV). And the comparison of the condition of the chromosomes in the early prophase of mitosis and meiosis shows that they divide during the resting stage in the mitotic cycle (Chs. II and XI).

The application of the comparative method enables us to take a more objective view of the nature of artefacts than is commonly done.

Artefact has been one of those words that " plainly force and overrule the understanding." An artefact is an appearance that arises from treatment. All living organisms are therefore liable to show artefacts when they are killed, and they may, as Belar (1928, pp. 3–4) pointed out, reveal " vital " artefacts while still showing signs of normal life, *e.g.*, the collapse of the chromosomes referred to above. These follow merely from manipulation. But in ordinary treatment manipulation is followed by fixation (coagulation and hardening) and staining (differential absorption of dyes). Both of these may lead to artefacts. The fact that stains are apparently of three degrees of directness : (i) those which stain cell-structure differentially in the first instance (*e.g.*, Giemsa), (ii) those which stain uniformly and are de-stained differentially (*e.g.*, gentian violet), (iii) those which are de-stained differentially after mordanting (*e.g.*, iron-hæmatoxylin), is probably not of great importance, for the decisive differential reaction is in all cases a single one, and judged by the results, under suitable conditions of fixation, it is of the same degree of specificity. The differences in effect of treatment are therefore almost entirely conditioned by differences in fixation to which staining is secondary.

No appearance of treated material is definitely free from artefact nor is any appearance " pure " artefact. The question is therefore not so much whether an appearance is an artefact but how significant the artefact is. For this purpose comparison enables us to distinguish those that are *characteristic* from those that are not, as follows :

(i) The collapse of the chromosomes to one side of the nucleus is characteristic of two stages of meiosis and is not found in the prophase of the abortive meiosis of parthenogenetic aphides (Morgan, 1912), although it is found in the normal prophase. The reason for this has been shown above. (ii) The chromomere structure of the early prophase chromosome is a characteristic artefact because homologous chromosomes in the same nucleus show similar chromomeres. (iii) The spiral structure seen after squeezing living chromosomes is characteristic, but the fractured structure seen when they are squeezed after fixation is not. (iv) The fibrillar structure of the shrunk spindle is characteristic and is derived from a special arrangement of differently hydrated particles in it. (v) The anastomosed structure seen in the resting nucleus by Sharp and Martens is non-characteristic. It cannot be related to structures seen earlier or later (Ch. II).

Having excluded non-characteristic artefacts, we may then consider the significance of different kinds of characteristic artefact. The comparative method at once shows us that some correspond closely with living conditions, *e.g.*, the chromomere structure, while others are definitely abnormal and peculiar to the effects of treatment on certain organisms, *e.g.*, the contraction in the prophase of meiosis.

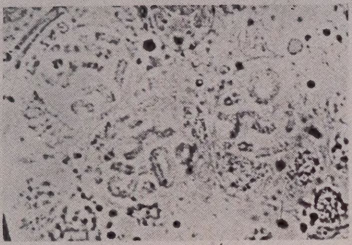
PLATE VIII

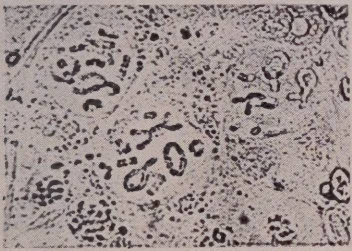
FIGS. 1–3.—Diakinesis in *Stenobothrus lineatus*. (From Belar, 1927.) Fig. 1. Living cells. Fig. 2. The same cells after fixation with osmium tetroxide vapour and Flemming. Fig. 3. The same cells after staining with Giemsa-Romanovsky.

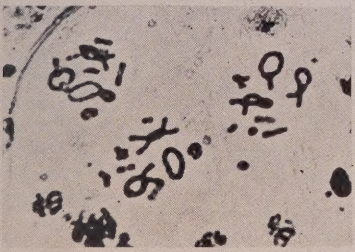
FIGS. 4–7.—Photographs of living chromosomes of *Melanoplus femur rubrum* (Orthoptera) at meiosis, taken by ultra-violet light. (After Lucas and Stark, 1931.)

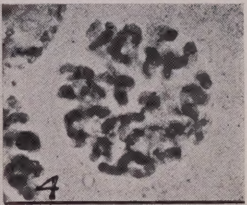
Fig. 4. Late telophase before meiosis. × 1800. Fig. 5. Pachytene. × 1800. Fig. 6. First anaphase. × 1200. Fig. 7. First telophase. × 1200.

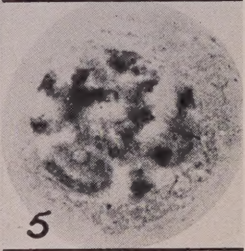
PLATE VIII

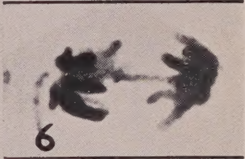

1

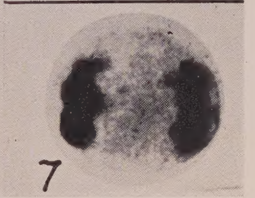

2


3


4


5


6


7

[*To face p.* 488.

Genetical inferences are subject to other kinds of error. They are derived from observations of mitosis and meiosis. In mitosis assumptions are made which are correct except for certain exceptional cases.

(i) It is assumed that the chromosome complement seen at one division is characteristic of the individual and even of the species. The exceptions to this rule (based on the theory of permanence) are so few that it can be satisfactorily applied in practice unless there are *a priori* reasons for expecting lack of constancy (as in the examination of mutants or geographical races).

(ii) It is assumed (also on the basis of the theory of permanence) that differences between species in the size of their chromosomes will be maintained in their hybrids and derivatives. The observations described earlier (Ch. III) show that this conclusion is not necessarily true, although experimental evidence is still confined to few and exceptional cases. Since genetic properties influence chromosome size and length where two related species have chromosomes of different size or length but are otherwise comparable, it is rather to be assumed that this difference is due to a genetic difference and that therefore the hybrid will fail to show it. But there is another restriction to this type of inference, *viz.*, the different effects of the same treatment on chromosomes of related species. Such different effects are probably responsible for the differences in the size of chromosomes observed by Farmer and Digby (1914) in diploid and tetraploid *Primula kewensis*, suggesting that the tetraploid was derived by transverse splitting of the chromosomes, and by Tischler (1928) between species of *Ribes*, suggesting that autosyndesis occurred in the hybrid (*cf.* Meurman, 1928; D., 1929 *d*), because large and small pairs of chromosomes were found there.

In meiosis, erroneous assumptions have been made and still are made with regard to the pairing of chromosomes, such as the following :—

(i) Pairing has been held to be determined by "affinity" between chromosomes (*cf.* Dobzhansky, 1931). It is therefore constant (under constant external conditions), and a few observations are an accurate measure of this "affinity." Chromosomes which do not pair are not "homologous." In this way a simple rule is made for analysing the relationships and even phylogeny of species. The conclusions derived from these imperfect assumptions are of doubtful value (*e.g.*, in *Nicotiana*). Even with quantitative analysis (*e.g.*, in *Triticum-Ægilops* hybrids) it is doubtful whether relationships can be accurately assessed because (*inter alia*) the differences in the chromosomes which reduce their pairing are not necessarily directly related to, and therefore proportional to, the differences which determine genetic differences in the organism (*v.* Ch. VI).

(ii) Ring-formation has been held (by adherents of the theory of telosynapsis) to be determined by an undefined "hybridity," a reduced

" homology," a genetic factor, and so on. These inferences were loose and unjustifiable and disagreed with genetic evidence (Ch. XI).

Summing up : The mechanical and genetical interpretations put on chromosome behaviour have suffered from two chief sources of error. First, the relative values of direct and comparative inference have not been correctly assessed. Direct inferences have been admitted as " facts " and " observations " or denied as " artefacts " and " misinterpretations " when actually their whole weight depended upon their use for comparative inference. Comparative inference, on the other hand, has too often been put aside as speculative and irrelevant when indeed it has been the only means for any general advance in the understanding of the processes concerned. Hypothesis based on it has often proved more reliable than the " facts " of direct observation.

Secondly, synthesis has preceded complete analysis. " The method of discovery and proof according to which the most general principles are first established, and then intermediate axioms are tried and proved by them, is the parent of error and the curse of all science " (*Novum Organum*, I, 69). This method has been particularly unfortunate in its application to the structural and genetical interpretation of meiosis. The relations between the several stages of any process must be determined before any interpretation of the whole can be attempted.

APPENDIX II

RECENT IMPROVEMENTS IN TECHNIQUE

Two recent advances in cytological technique have revolutionised the study of the chromosomes in plants.

The first is the use of smears for pollen mother-cells as well as for spermatocytes. This method gives superior fixation with the certainty of observing complete nuclei. It can also be used for more extensive work on account of its quicker procedure.

The second is the use of more transparent stains which allow sections to be cut very much thicker. For the somatic chromosomes of *Fritillaria* or *Tradescantia* sections need to be cut at 40μ, and they can be cut at this thickness if gentian violet is used as the stain. In such cases it is clearly a mistake to suppose that the most pleasing contrast between chromosomes and cytoplasm is also the most useful. A faded slide is often best.

These two improvements therefore have made it possible to study the largest chromosomes with greater accuracy than hitherto, and this has been of vital importance in increasing the accuracy of observation, for it is only in the larger chromosomes that we have any chance of determining the principles of chromosome organisation and behaviour.

Finally, the standard of plant cytology has greatly improved with the decline of alcoholic fixatives such as Carnoy's. It is now recognised that a dehydrating fixative should only be used in the last resort. Non-alcoholic fixatives are nearly always satisfactory for root-tips, and can be used for most pollen mother-cells provided that the anthers are dissected out before fixation—a task in which no trouble should be spared. (Once the tissue is fixed the damage is done ; after-treatment is relatively unimportant.) Fixation and washing may then be curtailed to three or four hours each instead of the traditional twelve or twenty-four.

These changes in technique have made it possible to bring the study of plant cytology to the high level attained earlier in animal work, and on account of the great scope afforded by plant variation the plant cytologist has been enabled to contribute the great bulk of recent advances in the subject.

The following is a list of references to authors who describe new methods of preparation.

Microscopy

Belling, 1930.
Lucas and Stark, 1931 (ultra-violet light).

General Technique

Taylor, 1928.
Belar, 1929 *c*.
Belling, 1930.
La Cour, 1931.

Fixation

Navashin, 1926 (chrom-formol-acetic).
La Cour, 1931 (various).
Sakamura, 1927 *b* (hot water).
Kihara, 1924, *cf.* Huskins, 1928 (Carnoy + Flemming).
Kihara, 1927 (cooling before fixing).

Smearing

Taylor, 1924 *a* (Flemming + hæmatoxylin).
Darlington, 1926 (Flemming + gentian violet).
Belling, 1926 *a* (iron aceto-carmine) ; *cf.* de Meijere, 1928, 1930.
Belar, 1929 *c* (osmic vapour + Flemming).
McClintock, 1929 *b* ; Steere, 1931 (permanent aceto-carmine).
Barrett, 1932 (aceto-hæmatoxylin).

Staining

Feulgen and Imhäuser, 1925 *et al.* (specific nuclear stain).
Newton and D., 1929 (gentian-violet-iodine).
Belling, 1930 (iron-brazilin).
Belar, 1929, *b* and *c* (Giemsa).
La Cour, 1931 (chromic acid as mordant after gentian violet).

Living Material

Chambers, 1925.
Schaede, 1925, 1927.
Sakamura, 1927 *a*.
Belar, 1929, *a*, *b*, and *c*.
Lucas and Stark, 1931.

APPENDIX III

GLOSSARY

Mit Worten lässt sich trefflich streiten.
GOETHE, *Faust*, I.

Note on Terminology

THE description of the chromosomes and the reproductive processes demands an international technical nomenclature. This has been changed and developed in recent years. Many terms unnecessarily Greek and obscure are falling into disuse, and geneticists who need to follow the essentials of cytological work are naturally impatient of its former baroque terminology. They find that the " heterotypic " and " homoeotypic " mitoses can just as well be described as " first " and " second " divisions. Terms recently introduced have therefore been for the most part self-explanatory and have not on this account lost anything in precision.

Terms not used in the text are enclosed in brackets. The usages given are those adopted in this book and are not always the original ones, since usage necessarily changes. For the sources of many of these the author is indebted to Wilson (1925), Rosenberg (1930), Carothers (1931), and a number of correspondents.

Allelomorph, one of two dissimilar factors which on account of their corresponding position in corresponding chromosomes are subject to alternative (mendelian) inheritance. *Bateson.*

Allopolyploid, a polyploid whose chromosomes do not usually form multivalents at meiosis but pair as far as their homologies allow them, *e.g.*, a tetraploid with $2x$ bivalents or a triploid with x bivalents and x univalents (*cf.* Autopolyploid). *Kihara* and *Ono*, 1926.

Allosyndesis, the pairing in a polyploid of chromosomes derived from opposite parents ; particularly as opposed to autosyndesis, in a hybrid between allopolyploids. *Ljungdahl*, 1922.

Alternation of Generations, the occurrence of two series of nuclear divisions in the life cycle, a haploid and a diploid.

Amitosis, the division of a nucleus without separation of daughter chromosomes. *Flemming*, 1882.

Amphimixis, the bringing together of elements from two gametes in fertilisation (as opposed to apomixis). *Weismann.*

Anaphase, the stage at which daughter chromosomes move apart in a nuclear division. *Strasburger*, 1884.

[**Anaschistic**], bivalents that are said to split " longitudinally " at the first meiotic division ; these are bivalents with chiasmata close to the spindle attachment (as opposed to diaschistic). *Farmer* and *Moore*, 1905.

Androgenesis, male parthenogenesis, *q.v.*

Aneuploid, having an uneven multiple of the basic number of chromosomes through purely numerical aberration—therefore an unbalanced polyploid. *Täckholm*, 1922.

Apogamy, apomixis involving the replacement of the gametes by unspecialised cells which do not fuse. *De Bary*, 1878 ; *Winkler*, 1908.

Apomixis, the occurrence of the external form of sexual reproduction with the omission of fertilisation and usually meiosis as well (as opposed to amphimixis). *Winkler*, 1908.

Apospory, apomixis involving the replacement of the spores by unspecialised cells which have not undergone meiosis. *Bower*, 1887 ; *cf. Winkler*, 1908 ; *Rosenberg*, 1930.

[**Atelomitic**], of chromosomes, having intercalary, as opposed to terminal, spindle attachments. *Carothers*, 1917.

Attachment, (i) the spindle attachment, *q.v.* ; (ii) the permanent fusion of two chromosomes. *L. V. Morgan*, 1922.

Autosomes, those chromosomes whose segregation does not normally affect the determination of sex (as opposed to sex-chromosomes).

Autosyndesis, the pairing, in a polyploid, of chromosomes derived from the same parent ; particularly its exceptional occurrence in an allopolyploid. *Ljungdahl*, 1922.

Balance, the condition in which the genes are adjusted in proportions which give satisfactory and normal development of the organism (opposite : unbalance). *Bridges*, 1922.

Secondary ——, a new balance derived by change in the proportion of genes, as in a secondary polyploid, from an old balance, and capable of competing with it. *D.* and *Moffett*, 1930.

Balanced Lethal Factors. *v. Lethal.*

Basic Number. The supposed number of chromosomes found in the gametes of a diploid ancestor of a polyploid.

Bivalent (*v.* Univalent).

Bouquet, the zygotene and pachytene stage in those organisms in which the chromosomes lie in loops with their ends near one part of the wall of the nucleus. *Eisen*, 1900.

Cell, a unit in the structure of the animal or plant containing one nucleus, or several where these are separated by a uniform substratum. *Leeuwenhoek*, *Schleiden* and *Schwann*.

Centrosome, the self-propagating body which during division in many organisms lies at the two poles of the spindle and appears to determine its orientation. *Boveri*, 1888.

Chiasma, -ta (Hellenistic Greek), an exchange of partners in a system of paired chromatids ; observed between diplotene and the beginning of the first anaphase in meiosis. *Janssens*, 1909.

Interstitial ——, where there is a length of chromatid on both sides of the chiasma. *D.*, 1929 *c*.

Terminal ——, where an exchange occurs amongst the distal particles of the chromatids. *D.*, 1929 *c*.

Multiple ——, a terminal chiasma where three or four pairs of chromatids are engaged. *D.*, 1929 *c*.

Lateral ——, a chiasma which is terminal as to two chromatids and interstitial as to the others. Of two kinds, symmetrical and asymmetrical. *D.*, 1929 *c*.

Compensating ——, where one chiasma restores the association interrupted by the other. *Newton* and *D.*, 1930.

Imperfect ——, where one of the four associations in a chiasma is broken prior to anaphase. *D.*, 1929 *c*.

[**Equational**] *v.* text.

Chiasma Theory of Pairing, the hypothesis that whenever two chromosomes which have been paired at pachytene remain associated until metaphase they do so by virtue of the formation of a chiasma or visible exchange of partners amongst their chromatids. *D.*, 1929, *b* and *c*.

Chiasmatype Hypothesis, the part of the chiasmatype theory which supposes that chiasmata are determined by crossing-over between two dissimilar chromatids of the four involved. *D.*, 1930 *b*.

Chiasmatype Theory, the theory that chiasmata are connected with crossing-over either as a cause or as a consequence. *Janssens*, 1909.

Chimæra, a plant composed of tissues of two genetically distinct types as a result of mutation, segregation, irregularity of mitosis, or artificial fusion (graft-hybrids), *v.* Mosaic. *Cf. Baur, Winkler.*

Chondriosomes, bodies in the cytoplasm which are believed to be self-propagating, including mitochondria and Golgi-bodies. *Benda*, 1904.

Chromatid, a half chromosome between early prophase and metaphase of mitosis and between diplotene and the second metaphase in meiosis—after which stages, *i.e.*, during an anaphase, it is known as a daughter-chromosome. The separating chromosomes at the first anaphase are known as daughter-bivalents, or, if single chromatids derived from the division of univalents, daughter-univalents. *McClung*, 1900.

Chromatin, the part of the chromosome that stains deeply during mitosis, as opposed to an achromatic part. The distinction is difficult to apply and is often of doubtful validity. *Flemming*, 1879.

[**Chromiole**], part of an artefact known as a chromomere, but actually produced by clumping of several chromomeres. *Eisen*, 1900.

Chromomeres, the smallest particles identifiable by their characteristic size and position in the chromosome thread between leptotene and pachytene. *Wilson*, 1896.

[**Chromonema, -ta**], the chromosome thread, *q.v.* (similarly leptonema, pachynema, etc., the chromosome threads at leptotene, pachytene, etc.). *Wilson*, 1896.

Chromosome Thread, the thread consisting of chromomeres, achromatic connective and, perhaps, pellicle at prophase; and constituting, as a spiral, the metaphase chromosome.

Chromosomes, the bodies into which the nucleus resolves itself at the beginning of mitosis and from which it is derived at the end of the mitosis.

Complement, the group of chromosomes derived from a particular nucleus in gamete or zygote, composed of one, two or more sets.

Condensation or **Contraction** of the chromosome, the thickening, shortening and spiralisation of the chromatids during prophase (*v.* Text).

Conjugation, pairing of chromosomes, gametes or zygotes, or fusion of pairs of nuclei.

Constriction, an apparent discontinuity of fixed position in the metaphase chromosome, probably due to a local straightening in the spiral.

Primary or **attachment** ——, that always associated with the spindle attachment.

Secondary ——, any other constriction. *D.*, 1926.

Crossing-over, the exchange of corresponding segments between corresponding chromatids of different chromosomes; a process inferred genetically from the reassociation of linked factors in mendelian hybrids and cytologically from the reassociation of parts of chromosomes in structural hybrids. *Morgan*, 1911.

Double ——, the production of a chromosome in which crossing-over has occurred twice; may be reciprocal or non-reciprocal as between chromatids at meiosis. *Sturtevant.*

[**Cytokinesis**], the separation of daughter cells, usually after mitosis.

Cytoplasm, the protoplasm apart from the nucleus.

Daughter chromosome (*v.* Chromatid).

Deficiency, loss or " deletion " of a segment of a chromosome from the diploid complement. *Bridges*, 1917.

Diakinesis, the last stage in the prophase of meiosis—immediately before the disappearance of the nuclear membrane. *Haecker*, 1897.

[**Diaschistic**], bivalents that are said to divide transversely at the first division; this is owing to the chromosomes being united by a single terminal or nearly terminal chiasma. *Farmer* and *Moore*, 1905.

[**Didiploid**], autotetraploid (*v.* Autopolyploid). *Nemec*, 1910.

Differential Affinity, the failure of two chromosomes to pair in the presence of a third although they pair in its absence. *D.*, 1928.

Diminution, the loss or expulsion of a part of the chromosome complement at mitosis so that a daughter nucleus is formed lacking this part.

Diploid, (i) the zygotic number of chromosomes ($2n$) as opposed to the gametic or haploid number (n); (ii) an organism having two sets of chromosomes ($2x$) as opposed to organisms having one (haploid) three (triploid) or more sets (x, $3x$, etc.) (*v.* Polyploid). *Strasburger*, 1905.

[**Diplont**], organism at the diploid stage of the life-cycle, as opposed to " haplont."

Diplophase, [(i)] the diplotene stage of meiosis; (ii) the diploid phase of the life-cycle, particularly in the Basidiomycetes where nuclear fusion does not immediately follow cell-fusion. *Goebel.*

Diplotene, the stage of meiosis which follows division of the chromosome at the pachytene stage. *v. Winiwarter*, 1900.

Disjunction, the separation of chromosomes at anaphase, particularly of the first meiotic division.

Distal, that part of a chromosome which relative to another part is further from the spindle attachment.

[**Duplication**] (*v.* Reduplication). *Bridges*, 1917.

Dyad, (i) the pair of cells formed after meiosis through irregularity instead of a quadruple " tetrad " (*q.v.*); [(ii)] the univalent chromosome, composed of two chromatids, at meiosis.

Embryo-sac, the female gametophyte in the angiosperms.

[**Ergastic**], of materials in the cell: the non-living products of metabolism (*e.g.*, many fats and carbohydrates). *A. Meyer*, 1896.

Factor, the hypothetical determinant of a character in respect of which an organism may show a mendelian difference. It is usually an abstract description of a gene which is capable of mutating. *Bateson* and *Punnett*, 1905.

Fertilisation, the fusion of two germ-cells and of their nuclei, without which their later development is usually impossible.

First Division, the first of the two meiotic divisions, formerly known as the " heterotypic " or " reduction " division.

Gametes, cells which are specialised for fertilisation and cannot normally develop without it.

Gametophyte, the haploid plant which produces the gametes where there is an alternation of generations.

Gene, the unit of reproduction and variation in the hereditary material. It may correspond with part or the whole of a chromomere. It is the genetical atom and is hypothetical to the same extent as the chemical atom used to be. *Johannsen*, 1911, 1923; *Morgan*, 1925.

[**Genome**], a chromosome set, *q.v.* *Winkler*, 1916.

Genotype, the kind or type of the hereditary properties of an organism. *Johannsen.*

Genotypic Control, the control of chromosome behaviour by the hereditary properties of the organism. *D.*, 1932 *a*.

Haploid (*v.* Diploid). *Strasburger*, 1905.

"**True** ——," an organism having one set of chromosomes (*v.* Text).

Haplo-diploid Sex Differentiation, that in which the sexes are distinguished by the male being haploid, the female diploid (*v.* Text).

[**Heterochromosomes**], chromosomes of exceptional form or behaviour, especially at meiosis, such as sex chromosomes, fragments, etc. *Montgomery*, 1904.

[**Heterogametic**], producing gametes of two kinds in regard to their properties of sex determination. *Wilson*, 1910.

Heterogamy, [(i)] differentiation of male and female types of gametes; (ii) the special differentiation by which in the hybrid *Œnothera* species two kinds of gametes of both sexes are produced, but opposite kinds function in opposite sexes. *Renner*, 1919.

[**Heteromorphic**], of chromosomes, unequal bivalents. *Carothers*, 1917.

[**Heteroploid**], all organisms that are not diploid. *Winkler*, 1916.

[**Heteropycnosis**], precocious condensation of certain chromosomes in the prophase especially of meiosis (*v.* Precocity). *Gutherz*, 1906.

[**Heterotypic Division**], the first meiotic division. *Flemming*, 1887.

Heterozygote, a zygote derived from the union of gametes dissimilar in respect of their chromosomes. *Bateson*, 1904. Used for narrower categories of hybrid, as: Mendelian, Interchange, Reduplication, Fragmentation, Translocation, and Deficiency Heterozygotes (*v.* Text).

Complex ——, one whose gametes have numerous differences which segregate as a unit. *Renner*, 1917.

Sex —— (a form of complex heterozygote), a zygote of the heterozygous sex, *v.* *Y* Chromosome (*v.* Text).

Heterozygous Sex (*v.* *Y* Chromosome).

[**Hexad**], unequal bivalent (not trivalent) formed by pairing of one chromosome with its homologue which has fused with a third non-homologous chromosome, in a fusion-heterozygote. *McClung*, 1917.

[**Homeotypic Division**], second division of meiosis. *Flemming*, 1887.

Homogametic Sex, the homozygous sex, *q.v.* *Wilson*, 1910.

Homology, the similarity of structures in different organisms which they owe to the common ancestry of the organisms. *Owen.*

Homozygote, a zygote derived from the union of gametes identical in respect of their chromosomes. *Bateson*, 1904.

Homozygous Sex (*v.* *X* and *Y* Chromosomes).

Hybrid, a heterozygote. Used for the broader categories as:

Numerical ——, one whose parental gametes differed in respect of the number of chromosomes. *D.*, 1931 *c*.

Structural ——, one whose parental gametes differed in respect of the structure of their chromosomes. *D.*, 1929 *c*.

Interchange, an exchange of non-homologous segments of non-homologous chromosomes, *v.* *Belling*, 1927 *b*. (The term "segmental interchange" is used by Belling to include crossing-over (*q.v.*), but the two are conveniently distinguished, *v.* Text).

Interference, the property by which the occurrence of one crossing-over reduces the chance of occurrence of another in its neighbourhood. *Muller*, 1916.

Cytological ——, the same property as between chiasmata. *Haldane*, 1931 *b*.

Interkinesis (*v*. Interphase, Resting Stage). *Grégoire*, 1905.

Interphase, the resting stage that may occur between the first and second divisions. Should not be applied to the resting stage in general. *Lundegårdh*, 1912.

Inversion, the reversal of the linear sequence of the genes in one segment of a chromosome relative to an adjoining segment. *Sturtevant*, 1926.

Isogamy, morphological similarity of gametes.

[**Karyokinesis**], *Schleicher*, 1878, = mitosis, *q.v.*

[**Karyolymph**], nuclear sap. *Haeckel*, 1891.

[**Karyology**], nuclear cytology.

[**Karyomere**], a compartment or vesicle in the resting nucleus, usually containing one chromosome.

[**Karyosphere**], part of the nucleus into which the chromosomes have contracted.

Leptotene, the single chromosome threads at the early stage of the prophase of meiosis, and by extension the stage itself, (*v*. Zygotene, Pachytene, Diplotene) *v. Winiwarter*, 1900.

Lethal Factors, factors which render inviable an organism possessing them in a homozygous condition.

Balanced —— ——, factors which lie in chromosomes of opposite gametes and do not frequently cross over at meiosis. The chromosomes concerned must be homologues except in a ring-forming interchange heterozygote. *Muller*, 1918, 1930 *b*.

Linin, a structural component of the nucleus. The term has been applied to the descriptions of various artefacts and has no definite meaning.

Localisation, the genetic property of restriction of chiasmata to one part of the paired chromosomes—proximal or distal. *D*., 1931 *c*.

Macronucleus, the large vegetative nucleus of the Infusoria.

Matroclinal Inheritance, that in which the offspring resembles the mother more closely than the father (as opposed to Patroclinal).

Maturation, the formation of gametes or spores by meiosis.

Megaspore (Macrospore), a spore having the property of giving gametophytes with only female gametes (the embryo-sac).

Meiosis, a form of mitosis in which the nucleus divides twice and the chromosomes once. The prophase of meiosis is the prophase of the first of the two divisions. *Farmer* and *Moore*, 1905.

Metabolic Stage, an unwarranted description of the resting stage, *q.v.*

Metaphase, the stage of mitosis or meiosis in which the chromosomes lie in a plane at right angles to the axis of the spindle and half-way between the poles. *Strasburger*, 1884.

[**Metasyndesis**] (*v*. Telosynapsis). *Haecker*, 1907.

Microchromosomes, fragment chromosomes in the Hemiptera which do not form chiasmata and do not usually pair until metaphase. *Wilson*, 1905.

Micronucleus, the small, permanent, reproductive nucleus of the Infusoria.

Microspore, the spore which produces a gametophyte bearing only male gametes (the pollen grain).

Mitosis, the process by which daughter chromosomes are separated into two groups ; the diagnostic property of division of the nucleus. The term may be conveniently used in contradistinction to meiosis. *Flemming*, 1882.

[**Monoploid**], "True Haploid," *q.v.*

Monosomic, a diploid organism lacking one chromosome of its proper complement (*v.* Trisomic, Tetrasomic).

Mosaic, in animals, the equivalent of a chimæra, *q.v.* In plants, a chimæra produced by repeated mutation.

Mother-cell, the cell with a diploid nucleus which by meiosis gives four haploid nuclei, *e.g.*, the spore mother-cell in Bryophyta and Pteridophyta, the microspore or pollen mother-cell and the megaspore or embryo-sac mother-cell in phanerogams. The sperm mother-cell is known as the *spermatocyte*, the egg mother-cell as the *oöcyte*, in animals. Many other terms, used in the lower plants, are unnecessary in general cytology.

Multivalent (*v.* Univalent).

[**Non-cellular**], unicellular organisms in the Protista. *Dobell.*

Non-disjunction, cytologically, the failure of separation of paired chromosomes at meiosis and their passage to the same pole ; genetically, any results that might be imputed to such an abnormality, although usually arising from the failure of pairing, or from multivalent formation. *Bridges*, 1914.

Nuclear sap, the fluid which is lost by the chromosomes as they contract during prophase and which fills up the space of the nucleus.

Nucleolus, a body in the nucleus which disappears and does not resolve itself into chromosomes at mitosis.

Nucleus, a cell body reproducing by mitosis. The most constant constituent of animal and plant cells. *Robert Brown*, 1831.

Oligopyrene, of spermatozoa, those deficient in chromosomes.

Oöcyte, egg mother-cell.

[**Orthoploid**], polyploid organisms with a number of balanced, complete, chromosome sets. *Cf.* Aneuploid. (Originally used for those with any even number of chromosomes, *v. Winkler*, 1916.)

Pachytene, the double thread (and the stage at which it occurs) produced by pairing of the chromosomes in the prophase of meiosis, *v. Winiwarter*, 1900.

Pairing of Chromosomes, (active) the coming together of chromosomes at zygotene or (passive) the continuance of their association at the first division metaphase.

Somatic ——, the lying of homologous chromosomes especially close to one another at metaphase of mitosis.

Secondary ——, the same phenomenon as seen amongst bivalents at meiosis. *D.*, 1928.

Parasynapsis, the association of chromosomes side by side observed at zygotene, as opposed to their alleged end-to-end association at this stage, or " telosynapsis." *Wilson*, 1912.

Parthenogenesis, a form of apomixis in which the female gamete develops without fertilisation. *Owen*, 1849.

Diploid ——, that in which meiosis has failed first.

Haploid ——, that in which fertilisation fails first.

Male ——, that in which the male nucleus develops into the embryo.

Phenotype, the external appearance produced by the reaction of an organism of a given genotype with a given environment. *Johannsen.*

Polar Bodies, the expelled products of the two divisions of the oöcyte nucleus in animals.

Polyploid, an organism with more than two sets of homologous chromosomes. The terms used are triploid, tetraploid, pentaploid, hexaploid, heptaploid, octoploid (for octaploid), nonaploid, decaploid, undecaploid (for hendecaploid), dodecaploid and so on. Higher multiples are best referred to as $14x$, $22x$ and so on (*v.* Haploid, Diploid and Tetraploid). *Winkler*, 1916.

Secondary ——, a homozygous allopolyploid in which some of the chromosomes in the basic set are reproduced more frequently than others. *D.* and *Moffett*, 1930.

Polysomic (*v.* Trisomic).

[**Post-reduction**], the alleged reduction of the number of chromosomes at the second meiotic division, as opposed to pre-reduction, their reduction at the first division. *Korschelt* and *Heider*, 1903.

Precocity, the property of the nucleus beginning prophase before the chromosomes have divided; characteristic of meiosis. *D.*, 1931, *b* and *c*.

Differential ——, the property of some chromosomes condensing in advance of the rest of the complement during prophase (*v.* Text).

[**Pro-chromosomes**], stainable material in the resting nucleus believed to give rise to the chromosomes at prophase, but more probably merely the relics of the telophase chromosomes. *Overton*, 1909.

Prophase, the stage in mitosis or meiosis from the appearance of the chromosomes to metaphase.

Prothallium, the gametophyte in the Pteridophyta.

[**Prothallus**], = Prothallium, *q.v.*

Protoplasm, that part of the living organism which is not dead (including the nucleus and cytoplasm). *Purkinje*, 1840; *Strasburger*, 1882.

Protoplast, the protoplasm of one cell. *Hanstein*, 1880.

Proximal, of a chromosome, a part that is nearer the spindle attachment than a particular other part.

[**Pseudo-reduction**], the apparent reduction in chromosome number brought about by pairing. *Rückert*, 1894.

Quadrivalent (*v.* Univalent).

Reduction, the halving of the chromosome number at meiosis and, by extension, its genetical concomitants. *Weismann*, 1887.

Double ——, the occurrence of a reductional division at both divisions in regard to particular parts of chromosomes; possible in some hybrids and polyploids; hence "equational exceptions." *D.*, 1929 *c*; *Haldane*, 1930 *a*.

Gametic ——, meiosis immediately before fertilisation.

Zygotic ——, meiosis immediately after fertilisation.

Reduction Division, formerly applied to the one of the meiotic divisions at which a particular author thought reduction and segregation occurred.

Reductional Division, a separation of homologous parts of chromosomes derived from opposite parents at anaphase of a first or second division.

Reductional Split, the same at diplotene. *Wenrich*, 1916.

Reduplication, the occurrence of one segment of a chromosome twice in the same complement.

Restitution Nucleus, a single nucleus formed through failure of the first division. *Rosenberg*, 1927.

Rings, chromosomes associated end to end in a ring, usually by terminal chiasmata; especially applied to diploid interchange heterozygotes where more than two chromosomes are so associated.

[**Satellite**], a trabant, *q.v.*

Segment, a portion of a chromosome which can conveniently be considered as a unit for a given purpose. *Cf. Belling*, 1927 *b*.

Segregation, the separation of chromosomes of paternal and maternal origin at meiosis and the separation of the differences observed genetically. *Bateson*.

Secondary ——, the segregation in an allopolyploid of differences between its ultimate diploid parents. *D.*, 1928.

[**Semi-heterotypic Division**], a first division which gives rise to a restitution nucleus following defective pairing. *Rosenberg*, 1927.

Set of Chromosomes, a minimum group of chromosomes derived from the gametic complement of a supposed ancestor.

Sex-Chromosome, one which in the heterozygous sex is mated with a dissimilar homologue ; the X and Y chromosomes, *q.v.* *Wilson,* 1906.

Sperm, Spermatozoon, the male gamete in animals.

Spermatocyte, sperm mother-cell.

Spindle, the axially differentiated part of the cytoplasm within which the spindle attachments of a chromosome are held during metaphase and anaphase.

Spindle Attachment, the point in a chromatid which moves first to the pole at anaphase.

[**Spireme**], the chromosomes during the prophase in mitosis or meiosis, and hence the prophase itself. Particularly used in the expression " continuous spireme " (*v.* Chs. XI, XIV). *Flemming,* 1882.

Spore, a cell specialised for reproduction but not for fertilisation. In the higher plants it is always the product of meiosis and gives rise immediately to gametes.

Sporophyte, the spore-producing diploid in the higher plants (*v.* Gametophyte).

[**Strepsitene**], late diplotene when the successive loops between chiasmata coming to lie at right angles give the appearance of merely twisting round one another ; a misnomer. *Dixon,* 1900.

Structure, the potentially permanent arrangement of the chromosomes or genes in the chromosomes. Hence, " structural change " and " structural hybrid." *D.,* 1929 *c.*

[**Synapsis**], (i) chromosome pairing at zygotene, also described as syndesis ; (ii) contraction of the chromosomes to one side of the nucleus at this stage or at diplotene (an artefact), also described as synizesis.

Syndiploidy, the fusion of nuclei to give a doubled chromosome number, especially in the divisions immediately preceding meiosis. *Strasburger,* 1907.

[**Syngamy**], fusion of gametes.

[**Telomitic**], of chromosomes, having terminal spindle attachments. *Carothers,* 1917.

Telophase, the last stage of mitosis, after movement of the chromosomes has ceased. *Heidenhain,* 1894.

[**Telosynapsis**] (*v.* Parasynapsis).

Terminal Affinity, the property by which chromosomes are held together end to end from diplotene till metaphase or brought together in this way at metaphase (*v.* Text).

Terminal Chiasma (*v.* Chiasma.)

Terminalisation, expansion of the association of the two pairs of chromatids on one side of a chiasma at the expense of that on the other side. So called because the resulting " movement " of the chiasma is usually if not always towards the ends of chromosomes. *D.,* 1929 *c.*

Arrest of ——, stoppage of the movement of a chiasma through the opposite segments distal to it being non-homologous (*v.* Text).

Tetrad, (i) quartet of cells formed by meiosis in a mother-cell ; [(ii)] the four chromatids making up a bivalent at meiosis (*v.* Dyad, Hexad). *Nemec,* 1910.

Tetraploid (*v.* Polyploid). *Nemec,* 1910.

Tetrasomic, an organism with four chromosomes of one type, usually otherwise a diploid ($2x + 2$).

Trabant (German), a segment of a chromosome, separated from the rest by one long constriction if terminal or two if intercalary ; usually so short that longitudinal contraction reduces it to a sphere before it attains the characteristic chromatid diameter.

Intercalary ——, one with full-size chromosome limbs on both sides of it.

Lateral ——, where the trabant is a branch of the chromosome.

Translocation, change in position of a segment of a chromosome to another part of the same chromosome or of a different chromosome. *Bridges*, 1917.

Triploid, an organism having three sets of chromosomes. *Nemec*, 1910.

Trisomic, an organism with three chromosomes of one type ; usually otherwise diploid ($2x + 1$). A diploid organism is said to be doubly trisomic, not tetrasomic, when it has the two extra chromosomes of two different types ($2x + 1 + 1$).

Secondary ——, a trisomic organism in which the extra chromosome is made up of two identical halves. *Belling*, 1927 *b*.

Tertiary ——, a trisomic organism in which the extra chromosome is made up of halves corresponding with the halves of different chromosomes in the normal set. *Belling*, 1927 *b*.

Trivalent (*v.* Univalent).

Univalent, a body at the first meiotic division corresponding with a single chromosome in the complement; especially when unpaired. Bivalent, Trivalent, Quadrivalent, Quinquevalent, Sexivalent, Septivalent, Octavalent (for Octovalent), etc., are associations of chromosomes held together between diplotene and metaphase of the first division by chiasmata. Similar associations of more than two including non-homologous chromosomes in structural hybrids should be described as " unequal bivalents," " associations " or " rings " of three, four, etc. (*v.* Hexad). The hybrid forms, " monovalent," " tetravalent," " pentavalent," " hexavalent," etc., used in chemistry should be avoided.

X-chromosome, the sex chromosome in regard to which one sex is homozygous ; this is said to be the homozygous sex.

Y-chromosome, the sex chromosome that is present and pairs with the *X* in one sex; this is said to be the heterozygous sex.

Zygote, the cell formed by the union of gametes and the individual derived from it (*cf.* Homozygote).

Zygotene, the pairing threads (and the stage at which they occur) in the prophase of meiosis. *v. Winiwarter*, 1900.

APPENDIX IV

BIBLIOGRAPHY

INTRODUCTION

The most important works on animal chromosomes in recent years are that of Janssens, on which he rested his theory of chiasmatypy, and that of Belar, in which he summarised the properties of nuclear division in the Protista. The Schraders have investigated special mechanisms, which, although of restricted occurrence, are of theoretical importance.

The great bulk of chromosome studies have been concerned with plants, and this is for several reasons. Great improvements of technique, which we owe chiefly to Belling, Taylor and Newton, have increased both the facility and accuracy of observation. Then the great practical importance of plant genetics has encouraged the study so rendered possible. This necessarily rests on a sound interpretation of mitotic chromosomes which we owe to Taylor and to Navashin and the Russian school. Following this has come a great advance in the interpretation of meiosis, which consisted in the first place in showing that the principles already discovered in animals apply equally to plants. For the interpretation of prophase pairing we are chiefly indebted to Newton; for the interpretation of metaphase pairing, to Belling.

Such are the foundations of our present position. Its details have been made up in various ways. Particularly important have been the studies of abnormal meiosis. Rosenberg and Karpechenko have shown the abnormalities of the mechanism in hybrids. Kihara, Maeda and others have applied quantitative methods to the study of chromosome pairing in both hybrids and pure forms. From this has sprung a more accurate technique of investigation which is transforming our knowledge both of chromosome mechanics and of the relationship of chromosome behaviour with crossing-over.

Finally, the study of the inheritance of abnormalities of chromosome behaviour, especially by Beadle, Lesley, and Frost, has opened a new chapter in the study of the chromosomes.

Another class of observations lies in the borderland between genetics and cytology and has provided the closest bond between certain aspects of the two. These are the observations of chromosomes and inheritance in *Drosophila*, after treatment with X-rays, by Muller and Painter, Stern and Dobzhansky.

Finally an important step has been made in the compilation of accurate and complete lists of chromosome numbers in plants by Tischler. These are an indispensable vade-mecum for the plant cytologist.

Beyond such important work there is a body of morphological studies which bulks very large in the more classical journals of all countries. It is often competent but is conducted without any knowledge of recent advances in the subject and without any attempt at genetical or comparative interpretation. It is to be hoped that in the course of time editors of these journals will harden their hearts to such contributions.

NOTE.—Reviews and general works are marked with an asterisk. The earlier works of some authors have been omitted and can be found from their later references. Articles by the present author are referred to in the text by the letter D.

AFZELIUS, K., 1928, Die Embryobildung bei Nigritella nigra. *Sv. Bot. Tidskr.*, **22,** 82–91.

AGAR, W. E., 1911, The spermatogenesis of Leptosiren paradoxa. *Quart. J. Micr. Sci.*, **67,** 1–44.

AGAR, W. E., 1914, Parthenogenetic and sexual reproduction in *Sinocephalus vetulus* and other Cladocera. *J. Genet.*, **3,** 179–194.

AGAR, W. E., 1920, *Cytology, with special reference to the Metazoan nucleus*. London.

*AGAR, W. E., 1923, The Male Meiotic Phase in two Genera of Marsupials (Macropus and Pentauroides). *Quart. J. Micr. Sci.*, **67,** 183–202.

ÅKERLUND, E., 1927, Ein *Melandrium*-Hermaphrodit mit weiblichen Chromosomenbestand. *Hereditas*, **10,** 153–159.

ALLEN, C. E., 1919, The Basis of Sex Inheritance in *Sphærocarpos*. *Proc. Amer. Phil. Soc.*, **58,** 298–316.

[illegible], . E., 1926, The Direct Results of Mendelian Segregation. *Proc. Nat. Acad. Sci*, **12,** 2–7.

*ALLEN, C. E., 1932, Sex-Inheritance and Sex-Determination. *Amer. Nat.*, **66**, 97–107.

ANDERSON, E. G., 1925, Crossing over in a case of attached X chromosomes in *Drosophila melanogaster*. *Genetics*, **10,** 403–417.

ANDERSON, E. G., 1929, Studies on a case of high non-disjunction in *Drosophila melanogaster*. *Z.I.A.V.*, **51**, 397–441.

ANDERSSON, I., 1927, Notes on some characters in Ferns subject to Mendelian inheritance. *Hereditas*, **9**, 157–179.

*ANDERSSON-KOTTÖ, I., 1931, The Genetics of Ferns. *Bibliogr. Genet.*, **8**, 269–294.

ANDERSSON-KOTTÖ, I., 1932, Observations on the Inheritance of Apospory and Alternation of Generations. *Sv. Bot. Tidskr.* (In the press.)

ANDERSSON-KOTTÖ, I., and GAIRDNER, A. E., 1931, Interspecific Crosses in the Genus *Dianthus*. *Genetica*, **13**, 77–112.

ANDREWS, F. M., 1915, Die Wirkung der Zentrifugalkraft auf Pflanzen. *Jahrb. wiss. Bot.*, **56**, 221–253.

*ANKEL, W. E., 1927, 1929, Neuere Arbeiten zur Zytologie der naturlichen Parthenogenese der Tiere. Sammelreferat. *Z.I.A.V.*, **45**, 232–278. **52**, 318–370.

ANKEL, W. E., 1930, Die atypische Spermatogenese von Janthina (Prosobranchia Ptenoglossa). *Zeits. Zellforsch. u. Mikr. Anat.*, **11**, 491–608.

ARTOM, C., 1928, Diploidismo e Tetraploidismo dell' Artemia salina. *V. Int. Kong. Vererb.*, **1**, 384–386.

AVDOULOV, N. P., 1931, Karyo-systematische Untersuchungen der Familie Gramineen. *Bull. Appl. Bot. Suppt.*, **44**.

AVERY, P., 1929, Chromosome Numbers and Morphology in Nicotiana IV. The Nature and Effects of Chromosomal Irregularities in N. alata var. grandiflora. *Univ. Calif. Pub. Bot.*, **11**, 265–284.

AVERY, P., 1930, Cytological Studies of Five Interspecific Hybrids of Crepis Leontodontoides. *Univ. Calif. Pub. Agr. Sci.*, **6**, 135–167.

BABCOCK, E. B., and CLAUSEN, J., 1929, Meiosis in two species and three hybrids of Crepis and its bearing on taxonomic relationship. *Univ. Calif. Pub. Agr. Sci.*, **2**, 401–432.

*BABCOCK, E. B., and NAVASHIN, M., 1930, The Genus Crepis. *Bibliogr. Genet.*, **6**, 1–90.

BAEHR, V. B. de, 1919, Recherches sur la maturation des œufs parthénogénétiques dans l'Aphis palmæ. *Cellule*, **30**, 315–353.

BANTA, A. M., SNIDER, K. G., and WOOD, T. R., 1926, Inheritance in parthenogenesis and in sexual reproduction in a cladoceran. *Proc. Soc. Exp. Biol. N.Y.*, **23**, 621–622.

BANTA, A. M., and WOOD, T. R., 1928, Inheritance in Parthenogenesis and in Sexual Reproduction in Cladocera. *V. Int. Kong. Vererb.*, **1**, 391–396.

BARRETT, W. C., 1932, Heidenhain's Hæmatoxylin used with the Smear Technic. *Stain Technology*, **7**, 63–64.

BARTLETT, H. H., 1915, Mutation en masse. *Amer. Nat.*, **49**, 129–148.

BAUCH, R., 1926, Untersuchungen über zweisporige Hymenomyceten. I. Haploide Parthenogenesis bei Camarophyllus virgineus. *Zeits. f. Bot.*, **18**, 337–387.

BEADLE, G. W., 1930, Genetical and Cytological Studies of Mendelian Asynapsis in Zea Mays. *Cornell Univ. Exp. Sta. (Ithaca) Mem.*, **129.**

BEADLE, G. W., 1931, A gene in maize for supernumerary cell divisions following meiosis. *Cornell Univ. Exp. Sta. (Ithaca) Mem.*, **135.**

BEADLE, G. W., 1932, A gene in *Zea Mays* for failure of cytokinesis during meiosis. *Cytologia*, **3**, 142–155.

BEHRE, K., 1929, Physiologische und zytologische Untersuchungen über Drosera. *Planta* **7**, 208–306.

BELAR, K., 1922, Untersuchungen an *Actinophrys sol* Ehrenberg. I. Die Morphologie des Formwechsels. *Arch. Prot.*, **46**, 1–96.

Belar, K., 1923, Uber den Chromosomenzyklus von parthenogenetischen Erdnematoden. *Biol. Zbl.*, **43,** 513–518.

Belar, K., 1925. Der Chromosomenbestand der *Melandrium*-Zwitter. *Z.I.A.V.*, **39,** 184–190.

Belar, K., 1926 *a*, Zur Cytologie von *Aggregata eberthi*. *Arch. Prot.*, **53,** 312–325.

*Belar, K., 1926 *b*, Der Formwechsel der Protistenkerne. *Erg. Fortschr. Zool.*, **6,** 235–652.

Belar, K., 1927, Beiträge zur Kenntnis des Mechanismus der indirekten Kernteilung. *Naturwiss.*, **36,** 725–733.

Belar, K., 1928 *a*, Über die Naturtreue des fixierten Präparats. *V. Int. Kong. Vererb.*, **1,** 402–407.

*Belar, K., 1928 *b*, *Die Cytologischen Grundlagen der Vererbung*. Berlin.

Belar, K., 1929 *a*, Beiträge zur Kausalanalyse der Mitose II. Untersuchungen an den Spermatocyten von Chorthippus (Stenobothrus) lineatus Panz. *Arch. f. Entwm.*, **118,** 359–484.

Belar, K., 1929 *b*, Beiträge zur Kausalanalyse der Mitose III. Untersuchungen an den Staubfaden, Haarzellen und Blattmeristemzellen von *Tradescantia virginica*. *Zeits. Zellforsch. u. mikr. Anat.*, **10,** 73–134.

*Belar, K., 1929 *c*, Die Technik der deskriptiven Cytologie. *Meth. wiss. Biol.*, **1,** 638–735.

Beliajeff, N. K., 1930, Die Chromosomenkomplexe und ihre Beziehung zur Phylogenie bei den Lepidopteren. *Z.I.A.V.*, **54,** 369–399.

Belling, J., 1921, The Behavior of homologous Chromosomes in a triploid Canna. *Proc. Nat: Acad. Sci.*, **7,** 197–201.

Belling, J., 1924 *a*, The distribution of Chromosomes in the pollen-grains of a triploid Hyacinth. *Amer. Nat.*, **58,** 440–446.

Belling, J., 1924 *b*, Detachment (Elimination) of chromosomes in *Cypripedium acaule*. *Bot. Gaz.*, **78,** 458–460.

Belling, J., 1925 *a*, Fracture of Chromosomes in Rye. *J. Hered.*, **16,** 360.

Belling, J., 1925 *b*, Homologous and similar chromosomes in diploid and triploid hyacinths. *Genetics*, **10,** 59–71.

Belling, J., 1925 *c*, The Origin of Chromosomal Mutations in *Uvularia*. *J. Genet.*, **15,** 245–266.

Belling, J., 1925 *d*, Chromosomes of Canna and of Hemerocallis. *J. Hered.*, **16,** 465–466.

Belling, J., 1926 *a*, The Iron-Acetocarmine Method of Fixing and Staining Chromosomes. *Biol. Bull.*, **50,** 160–162.

Belling, J., 1926 *b*, Single and Double Rings at the Reduction Division in *Uvularia*. *Biol. Bull.*, **50,** 355–363.

Belling, J., 1926 *c*, The Structure of Chromosomes. *J. Exp. Biol.*, **3,** 145–147.

Belling, J., 1927 *a*, Configurations of Bivalents of Hyacinthus with regard to Segmental Interchange. *Biol. Bull.*, **52,** 480–487.

Belling, J., 1927 *b*, The Attachments of Chromosomes at the Reduction Division in the Flowering Plants. *J. Genet.*, **18,** 177–205.

Belling, J., 1928 *a*, A Method for the Study of Chromosomes in Pollen-Mother-Cells. *Univ. Calif. Pub. Bot.*, **14,** 293–299.

Belling, J., 1928 *b*, Nodes and Chiasmas in the Bivalents of *Lilium* with regard to segmental interchange. *Biol. Bull.*, **54,** 465–470.

Belling, J., 1928 *c*, A Working Hypothesis for Segmental Interchange between Homologous Chromosomes in Flowering Plants. *Univ. Calif. Pub. Bot.*, **14,** 283–291.

Belling, J., 1928 *d*, The Ultimate Chromomeres of Lilium and Aloë with Regard to the Number of Genes. *Univ. Calif. Pub. Bot.*, **14,** 307–318.

Belling, J., 1928 *e*, Contraction of Chromosomes during Maturation Divisions in Lilium and Other Plants. *Univ. Calif. Pub. Bot.*, **14**, 335–343.

Belling, J., 1929, Nodes and Internodes of Trivalents of Hyacinthus. *Univ. Calif. Pub. Bot.*, **14**, 379–388.

Belling, J., 1930, *The Use of the Microscope.* New York. (McGraw Hill.)

Belling, J., 1931 *a*, Chromomeres of Liliaceous Plants. *Univ. Calif. Pub. Bot.*, **16**, 153–170.

Belling, J., 1931 *b*, Chiasmas in Flowering Plants. *Univ. Calif. Pub. Bot.*, 311–338.

Belling, J., and Blakeslee, A. F., 1923, The Reduction Division in Haploid, Diploid, Triploid and Tetraploid Daturas. *Proc. Nat. Acad. Sci.*, **9**, 106–111.

Belling, J., and Blakeslee, A. F., 1924 *a*, The Distribution of Chromosomes in Tetraploid Daturas. *Amer. Nat.* **58**, 60–70.

Belling, J., and Blakeslee, A. F., 1924 *b*, The configurations and sizes of the chromosomes in the trivalents of 25-chromosome Daturas. *Proc. Nat. Acad. Sci.*, **10**, 116–120.

Belling, J., and Blakeslee, A. F., 1926, On the attachment of non-homologous chromosomes at the reduction division in certain 25-chromosome Daturas. *Proc. Nat. Acad. Sci.*, **12**, 7–11.

Belling, J., and Blakeslee, A. F., 1927, The Assortment of Chromosomes in Haploid Daturas. *Cellule*, **37**, 353–365. (*See also :* Blakeslee.)

Berg, K. H. v., 1931 *a*, Ein Bastard mit vier vollständigen haploiden Artgenomen. *Ak. Anz.* (Vienna), **22.**

Berg, K. H. v., 1931 *b*, Autosyndese in *Ægilops triuncialis* L. x *Secale cereale* L. *Zeits. f. Zücht.*, **17**, 55–69.

Bergner, A. D., and Blakeslee, A. F., 1932, Cytology of the Ferox-Quercifolia-Stramonium triangle in *Datura*. *Proc. Nat. Acad. Sci.*, **18**, 151–159.

Blackburn, K. B., 1924, The cytological aspects of the determination of sex in diœcious forms of Lychnis. *J. Exp. Biol.*, **1**, 413–430.

Blackburn, K. B., 1928, Chromosome Number in Silene and the Neighbouring Genera. *V. Int. Kong. Vererb.*, **1**, 439–446.

Blackburn, K. B., and Harrison, J. W. H., 1921, The Status of the British Rose Forms as determined by their Cytological Behaviour. *Ann. Bot.*, **35**, 159–188.

Blackburn, K. B., and Harrison, J. W. H., 1924, A Preliminary Account of the Chromosomes and Chromosome Behaviour in the *Salicaceæ*. *Ann. Bot.*, **38**, 361–378.

Blakeslee, A. F., 1922, Variations in Datura due to Changes in Chromosome Number. *Amer. Nat.*, **56**, 16–31.

Blakeslee, A. F., 1928, Genetics of *Datura*. *V. Int. Kong. Vererb.*, **1**, 117–130.

Blakeslee, A. F., 1929, Cryptic types in *Datura*. *J. Hered.*, **20**, 177–190.

Blakeslee, A. F., 1931, *Quoted in* An. Rep. of Director, Dept. of Genetics, Carnegie Inst. *Carnegie Inst. Yearbk.*, **29**, 35–68 (*v*. pp. 35–40, 43, 44).

Blakeslee, A. F., 1931, Extra Chromosomes, a Source of Variations in the Jimson weed. *Smithson. Rep.*, 1930, 431–450.

Blakeslee, A. F., Belling, J., and Farnham, A., 1923, Inheritance in Tetraploid Daturas. *Bot. Gaz.*, **76**, 329–373.

Blakeslee, A. F., Belling, J., Farnham, A., and Bergner, D., 1922, A haploid mutant in the Jimson weed, " Datura Stramonium." *Science*, **55**, 646–647.

Blakeslee, A. F., and Cleland, R. E., 1930, Circle Formation in Datura and Œnothera. *Proc. Nat. Acad. Sci.*, **16**, 177–183.

Blakeslee, A. F., Morrison, G., and Avery, A. G., 1927, Mutations in a Haploid Datura, and their bearing on the hybrid-origin theory of Mutants. *J. Hered.*, **18,** 193–199.

Bleier, H., 1928 *a*, Zytologische Untersuchungen an seltenen Getreide- und Rübenbastarden. *V. Int. Kong. Vererb.*, **1,** 447–452.

Bleier, H., 1928 *b*, Karyologische Untersuchungen an Linsen-Wicken Bastarden. *Genetica*, **11,** 111–118.

Bleier, H., 1930 *a*, Untersuchungen über das Verhalten der verchiedenen Kernkomponenten bei der Reduktionsteilung von Bastarden. *Cellule*, **40,** 85–144.

Bleier, H., 1930 *b*, Experimentell-cytologische Untersuchungen I. Einfluss abnormale Temperatur auf die Reduktionsteilung. *Zeits. f. Zellf. u. mikr. Anat.*, **11,** 218–236.

Bleier, H., 1931, Zur Kausalanalyse der Kernteilung. *Genetica*, **13,** 27–76.

Bonnier, G., 1923, Studies on High and Low Non-Disjunction in Drosophila melanogaster. *Hereditas*, **4,** 81–110.

Boring, A. M., 1907, A study of spermatogenesis of twenty-two species of the Membracidæ, Jassidæ, Ceropidæ and Fulgoridæ, with special reference to the behavior of the odd chromosome. *J. Exp. Zool.*, **4,** 469–512.

Bouin, P., 1925, Les cinèses de maturation et la double spermatogenèse chez *Scolopendra cingulata* L. *Cellule*, **35,** 371–423.

*Boveri, T., 1904, Ergebnisse über die Konstitution der chromatischen Substanz des Zellkerns. Jena.

Boveri, T., 1907, Zellenstudien VI. Die Entwicklung dispermer Seeigel-eier. Ein Beitrag zur Befruchtungslehre und zur Theorie des Kerns. *Jena Zeitschr.*, **37** (**43**), 1–292.

Boveri, T., 1909, Die Blastomerenkerne von Ascaris megalocephala und die Theorie der Chromosomenindividualität. *Arch. f. Zellforsch.*, **3,** 181–268.

Boveri, T., 1911, Über das Verhalten der Geschlechtschromosomen bei Hermaphroditismus. Beobachtungen an Rhabditis nigrovenosa. *Verh. Phys.-Med. Ges. Würzburg*, **41,** 83–97.

Bowen, R. H., 1924, Studies on insect spermatogenesis VI. Notes on the formation of the sperm in coleoptera and aptera, with a general discussion of flagellate sperms. *J. Morphol.*, **39,** 351–413.

Brauer, A., 1928, Spermatogenesis of Bruchus quadrimaculatus (Coleoptera ; Bruchidæ). *J. Morphol.*, **46,** 217–239.

Bremer, G., 1923, A cytological investigation of some species and species hybrids within the genus *Saccharum*. *Genetica*, **5,** 97–148, 273–326.

Bremer, G., 1924, The cytology of the sugar cane. *Genetica*, **6,** 497–525.

Bremer, G., 1925, The cytology of the sugar cane. Third contribution. *Genetica*, **7,** 293–322.

Bremer, G., 1930, The Cytology of Saccharum. *Proc. 3rd Cong. Int. Soc. Sugar Cane Tech.*, Sourabaya, 408–415.

Breslawetz, L., 1929, Zytologische Studien über Melandrium album L. *Planta*, **7,** 444–460.

Bridges, C. B., 1914, Direct Proof through Non-disjunction that the Sex-linked Genes of Drosophila are borne by the X-Chromosome. *Science* n.s., **40,** 107–109.

Bridges, C. B., 1916, Non-disjunction as a proof of the chromosome theory of heredity. *Genetics*, **1,** 1–52, 107–163.

Bridges, C. B., 1917, Deficiency. *Genetics*, **2,** 445–465.

Bridges, C. B., 1919, Duplication. *Anat. Rec.*, **15,** 357–358. (Abs. Proc. Amer. Soc. Zool.)

Bridges, C. B., 1921 *a*, Triploid Intersexes in *Drosophila melanogaster*. *Science*, **54,** 252–254.

BRIDGES, C. B., 1921 *b*, Genetical and Cytological Proof of Non-disjunction of the Fourth Chromosome of Drosophila melanogaster. *Proc. Nat. Acad. Sci.*, **7**, 186–192.

BRIDGES, C. B., 1922, The Origin of Variations in Sexual and Sex-limited Characters. *Amer. Nat.*, **56**, 51–63.

BRIDGES, C. B., 1923, The translocation of a section of chromosome I upon chromosome III in *Drosophila*. *Anat. Rec.*, **24**, 426–427. (Abs. Proc. Amer. Soc. Zool.)

BRIDGES, C. B., 1925 *a*, Sex in relation to chromosomes and genes. *Amer. Nat.*, **59**, 127–137.

BRIDGES, C. B., 1925 *b*, Elimination of Chromosomes due to a mutant (minute-n) in *Drosophila melanogaster*. *Proc. Nat. Acad. Sci.*, **11**, 701–706.

BRIDGES, C. B., 1925 *c*, Haploidy in *Drosophila melanogaster*. *Proc. Nat. Acad. Sci.*, **11**, 706–711.

BRIDGES, C. B., 1927 *a*, The Relation of the Age of the Female to Crossing Over in the Third Chromosome of Drosophila melanogaster. *J. Gen. Physiol.*, **8**, 689–700.

BRIDGES, C. B., 1927 *b*, Constrictions in the Chromosomes of Drosophila melanogaster. *Biol. Zbl.*, **47**, 600–603.

BRIDGES, C. B., 1929, Variation in crossing-over in relation to age of female in *Drosophila melanogaster*. Carn. Inst., Washington, 399.

BRIDGES, C. B., and ANDERSON, E. G., 1925, Crossing over in the X chromosomes of triploid females of *Drosophila melanogaster*. *Genetics*, **10**, 418–441. (*See also :* T. H. Morgan.)

BRIEGER, F., 1928, Über die Vermehrung der Chromosomenzahl bei dem Bastard *Nicotiana tabacum* L. x *N. Rusbyi* Britt. *Z.I.A.V.*, **47**, 1–53.

*BRIEGER, F., 1930 *a*, Selbststerilität und Kreuzungssterilität. *Monog. Gesamt. d. Phys. Pfl. u. Tiere*, **21** (Berlin).

BRIEGER, F., 1930 *b*, Über die Bedeutung der Chromosomenverdoppelung für das Problem der Artentstehung. *Ber. Deuts. Bot. Ges.*, **48**, 95–98.

BRUNELLI, G., 1910, La spermatogenesi della Tryxalis. IA. Divisioni spermatogoniali. *Mem. Soc. Ital. Sci.*, Ser. III, **16**, 221–236.

BRUNELLI, G., 1911, La spermatogenesi della Tryxalis : Divisioni maturative. *Mem. Acad. Lincei*, Ser. 5, **8**, 634–652.

BRUUN, H., 1930, The cytology of the genus Primula. A preliminary report. *Sv. Bot. Tidskr.*, **24**, 468–475.

BURNHAM, C. R., 1930, Genetical and Cytological Studies of Semisterility and Related Phenomena in Maize. *Proc. Nat. Acad. Sci.*, **16**, 269–277.

BUXTON, B. H., and DARLINGTON, C. D., 1932, Behaviour of a New Species, *Digitalis mertonensis*. *New Phytol.* (In the Press.)

BUXTON, B. H., and NEWTON, W. C. F., 1928, Hybrids of *Digitalis ambigua* and *Digitalis purpurea*, their Fertility and Cytology. *J. Genet.*, **19**, 269–279.

BYTINSKI-SALZ, H., and GÜNTHER, A., 1930, Untersuchungen an Lepidopterenhybriden, I. Morphologie und Cytologie einiger Bastarde der Celerio hybr. galliphorbiae-Gruppe. *Z.I.A.V.*, **53**, 153–234.

CAPINPIN, J. M., 1930, Chromosome Behaviour of Triploid Œnothera. *Nature*, **126**, 469–470.

CAROTHERS, E. E.; 1913, The Mendelian ratio in relation to certain orthopteran chromosomes. *J. Morphol.*, **24**, 487–511.

CAROTHERS, E. E., 1917, The Segregation and Recombination of Homologous Chromosomes as found in two genera of Acrididæ (Orthoptera). *J. Morphol.*, **28**, 445–520.

CAROTHERS, E. E., 1921, Genetical behavior of heteromorphic homologous chromosomes of *Circotettix* (Orthoptera). *J. Morphol.*, **35**, 457–483.

CAROTHERS, E. E., 1931, The Maturation Divisions and Segregation of Heteromorphic Homologous Chromosomes in Acrididæ (Orthoptera). *Biol. Bull.*, **61**, 324–349.

CARROLL, M., 1920, An extra dyad and an extra tetrad in the spermatogenesis of Camnula pellucida (Orthoptera); numerical variations in the chromosome complex within the individual. *J. Morphol.*, **34**, 375–455.

CASTLE, W. E., 1930, The Quantitative Theory of Sex and the Genetic Character of Haploid Males. *Proc. Nat. Acad. Sci.*, **16**, 783–791.

CATCHESIDE, D. G., 1931 *a*, Meiosis in a triploid *Œnothera*. *J. Genet*, **24**, 145–163.

CATCHESIDE, D. G., 1931 *b*, Critical Evidence of Parasynapsis in *Œnothera*. *Proc. Roy. Soc. B.*, **109**, 165–184.

CATCHESIDE, D. G., 1932, The Chromosomes of a New Haploid Œnothera. *Cytologia*, **3**. (In the press.)

CHAMBERS, R., 1925, The physical structure of protoplasm as determined by micro-dissection and injection, in: Cowdry, *General Cytology* (2nd imp. Chicago), 235–309.

CHAMBERS, R., and SANDS, H. C., 1923, A dissection of the chromosomes in the pollen mother cells of *Tradescantia virginica* L. *J. Gen. Physiol.*, **5**, 815–819.

CHAMPY, C., 1923, La spermatogenèse chez Discoglossus pictus (Otth.). Comparaison avec celles des autres Discoglossides et des Vertébrés en général. *Arch. Zool. Exp. Gen.*, **62**, 1–52.

CHIARUGI, A., 1926, Aposporia e apogamia in " Artemisia nitida " Bertol. *N. Giorn. Bot. Ital. N.S.*, **33**, 501–626.

CHIARUGI, A., 1929, Diploidismo con amfimissia e tetraploidismo con apomissia in una medesima specie *Nigritella nigra*. Reichb. *Boll. Soc. Ital. Biol. Sper.*, **4**(**6**), 1–3.

CHIARUGI, A., and FRANCINI, E., 1930, Apomissia in " Ochna serrulata " Walp. *N. Giorn. Bot. Ital. N.S.*, **37**, 1–250.

CHICKERING, A. M., 1927, Spermatogenesis in the Belostomatidæ. II. *J. Morphol.*, **44**, 541–607.

CHIPMAN, R. H., 1925, A study of synizesis and synapsis in Lilium superbum. *Amer. J. Bot.*, **12**, 1–18.

CHIPMAN, R. H., and GOODSPEED, T. H., 1927, Inheritance in Nicotiana Tabacum, VIII. Cytological features of purpurea haploid. *Univ. Calif. Pub. Bot.*, **11**, 141–158.

CHODAT, R., 1925, La chiasmatypie et la cinèse de maturation dans l'Allium ursinum. *Bull. Soc. Bot. Genève*, 1925, 1–30.

CLAUSEN, J., 1926, Genetical and Cytological Investigations on *Viola tricolor* L. and *Viola arvensis* Murr. *Hereditas*, **8**, 1–157.

CLAUSEN, J., 1927, Chromosome Number and the Relationship of Species in the Genus *Viola*. *Ann. Bot.*, **41**, 677–714.

CLAUSEN, J., 1929, Chromosome Number and Relationship of some North American Species of *Viola*. *Ann. Bot.*, **43**, 741–764.

CLAUSEN, J., 1930, Male sterility in *Viola Orphanidis*. *Hereditas*, **14**, 53–72.

CLAUSEN, J., 1931 *a*, Genetic Studies in *Polemonium*. III. Preliminary Account of the Cytology of Species and Specific Hybrids. *Hereditas*, **15**, 62–66.

CLAUSEN, J., 1931 *b*, Viola canina L., a cytologically irregular species. *Hereditas*, **15**, 67–88.

CLAUSEN, J., 1931 *c*, Cyto-genetic and Taxonomic Investigations in Melanium Violets. *Hereditas*, **15**, 219–308.

CLAUSEN, R. E., 1928, Interspecific Hybridization in Nicotiana VII. The cytology of hybrids of the synthetic species, Digluta, with its parents, Glutinosa and Tabacum. *Univ. Calif. Pub. Bot.*, **11,** 177–211.

CLAUSEN, R. E., 1930, Inheritance in *Nicotiana Tabacum*. X. Carmine-Coral Variegation. *Cytologia*, **1,** 358–368.

CLAUSEN, R. E., 1931 *a*, Inheritance in Nicotiana Tabacum. XI. The Fluted Assemblage. *Amer. Nat.*, **65,** 316–331.

CLAUSEN, R. E., 1931 *b*, Inheritance in Nicotiana tabacum. XII. Transmission features of carmine coral variegation. *Zeits. f. Zücht.* A., **17,** 108–115.

CLAUSEN, R. E., and GOODSPEED, T. H., 1925, Interspecific Hybridization in *Nicotiana* II. A Tetraploid *Glutinosa-Tabacum* hybrid, an experimental verification of Winge's Hypothesis. *Genetics*, **10,** 279–284.

CLAUSEN, R. E., and LAMMERTS, W. E., 1929, Interspecific Hybridization in Nicotiana X. Haploid and Diploid Merogony. *Amer. Nat.*, **63,** 279–282.

CLAUSEN, R. E., and MANN, M. C., 1924, Inheritance in Nicotiana Tabacum V. The occurrence of haploid plants in interspecific progenies. *Proc. Nat Acad. Sci.*, **10,** 121–124. (*See also :* Goodspeed.)

CLELAND, R. E., 1922, The reduction divisions in the pollen mother cells of *Œnothera franciscana*. *Amer. J. Bot.*, **9,** 391–413.

CLELAND, R. E., 1926 *a*, Meiosis in the pollen mother cells of *Œnothera biennis* and *Œnothera biennis sulfurea*. *Genetics*, **11,** 127–162.

CLELAND, R. E., 1926 *b*, Cytological Studies of Meiosis in anthers of *Œnothera muricata*. *Bot. Gaz.*, **82,** 55–70.

CLELAND, R. E., 1928, The Genetics of Œnothera in Relation to Chromosome Behavior, with Special Reference to Certain Hybrids. *V. Int. Kong. Vererb.*, **1,** 554–567.

CLELAND, R. E., 1929, Chromosome behavior in the pollen mother cells of several strains of *Œnothera Lamarckiana*. *Z.I.A.V.*, **51,** 126–145.

CLELAND, R. E., and BLAKESLEE, A. F., 1930, Interaction between complexes as evidence for segmental interchange in Œnothera. *Proc. Nat. Acad. Sci.*, **16,** 183–189.

CLELAND, R. E., and BLAKESLEE, A. F., 1931, Segmental Interchange, the Basis of Chromosomal Attachments in *Œnothera*. *Cytologia*, **2,** 175–233.

CLELAND, R. E., and OEHLKERS, F., 1929, New Evidence bearing upon the Problem of the Cytological Basis for Genetical Peculiarities in the Œnotheras. *Amer. Nat.*, **63,** 497–510.

CLELAND, R. E., and OEHLKERS, F., 1930, Erblichkeit und Zytologie verschiedener Œnotheren und ihrer Kreuzungen. *Jahrb. Wiss. Bot.*, **73,** 1–124.

COLLINS, G. N., and KEMPTON, I. H., 1916, Patrogenesis. *J. Hered.*, **7,** 106–118.

COLLINS, J. L., HOLLINGSHEAD, L., and AVERY, P., 1929, Interspecific Hybrids in *Crepis* III. Constant fertile forms containing chromosomes derived from two species. *Genetics*, **14,** 305–320.

COLLINS, J. L., and MANN, M. C., 1923, Interspecific Hybrids in *Crepis* II. A preliminary report on the results of hybridizing *Crepis setosa* Hall with *C. capillaris* (L.) Wallr. and *C. biennis* L. *Genetics*, **8,** 212–232.

CONKLIN, E. G., 1925, Cellular Differentiation, in : Cowdry, *General Cytology* (2nd imp. Chicago), 1925, 537–607.

COOPER, D. C., 1931, Microsporogenesis in *Buginvillæa glabra*. *Amer. J. Bot.*, **18,** 337–358.

COOPER, D. C., and BRINK, R. A., 1931, Cytological evidence for segmental interchange between non-homologous chromosomes in Maize. *Proc. Nat. Acad. Sci.*, **17,** 334–338.

*Correns, C., 1928, Bestimmung, Vererbung und Verteilung des Geschlechtes bei den Höhern Pflanzen. *Handbuch der Vererbungswissenschaft*, **2**.

Crane, M. B., and Darlington, C. D., 1927, The Origin of New Forms in Rubus. *Genetica*, **9**, 241–278.

Crane, M. B., and Darlington, C. D., 1932, Chromatid Segregation in Tetraploid *Rubus*. *Nature*, **129.**

Crane, M. B., and Gairdner, A. E., 1923, Species Crosses in *Cochlearia* with a preliminary account of their Cytology. *J. Genet.*, **13**, 187–200.

Crane, M. B., and Lawrence, W. J. C., 1929, Genetical and Cytological Aspects of Incompatibility and Sterility in Cultivated Fruits. *J. Pomol.*, **7**, 276–301.

Crane, M. B., and Lawrence, W. J. C., 1930, Fertility and Vigour of Apples in Relation to Chromosome Number. *J. Genet.*, **22**, 153–163.

Crane, M. B., and Zilva, S. S., 1931, The Antiscorbutic Vitamin of Apples, IV. *J. Pomol.*, **9**, 228–231.

Creighton, H. B., and McClintock, B., 1931, A Correlation of Cytological and Genetical Crossing-Over in Zea Mays. *Proc. Nat. Acad. Sci.*, **17**, 492–497.

Cretschmar, M., 1928, Das Verhalten der Chromosome bei der Spermatogenese von Orgyia thyellina Btl. und antiqua L. sowie eines ihrer Bastarde. *Zeits. Zellforsch. u. mikr. Anat.*, **7**, 290–399.

Dahlgren, K. V. O., 1927, Die Befruchtungerserscheinungen der Angiospermen, eine monographische Übersicht. *Hereditas*, **10**, 169–229.

Dahlgren, K. V. O., 1930, Zur Embryologie der Saxifragoideen. *Sv. Bot. Tids.*, **24**, 429–448.

Dark, S. O. S., 1931, Chromosome Association in Triploid *Primula sinensis*. *J. Genet.*, **25**, 91–96.

Darlington, C. D., 1926 *a*, Chromosome Studies in the Scilleæ. *J. Genet.*, **16**, 237–251.

Darlington, C. D., 1927, The Behaviour of Polyploids. *Nature*, **119**, 390.

Darlington, C. D., 1928, Studies in *Prunus*, I and II. *J. Genet.*, **19**, 213–256.

Darlington, C. D., 1929 *a*, Ring-formation in *Œnothera* and Other Genera. *J. Genet.*, **20**, 345–363.

Darlington, C. D., 1929 *b*, Meiosis in Polyploids II. *J. Genet.*, **21**, 17–56.

Darlington, C. D., 1929 *c*, Chromosome Behaviour and Structural Hybridity in the *Tradescantiæ*. *J. Genet.*, **21**, 207–286.

*Darlington, C. D., 1929 *d*, Polyploids and Polyploidy. *Nature*, **124**, 62–64, 98–100.

Darlington, C. D., 1930 *a*, Studies in *Prunus* III. *J. Genet.*, **22**, 65–93.

Darlington, C. D., 1930 *b*, A Cytological Demonstration of "Genetic" Crossing-Over. *Proc. Roy. Soc.* B, **107**, 50–59.

Darlington, C. D., 1930 *c*, Chromosome Studies in *Fritillaria*, III. Chiasma Formation and Chromosome Pairing in *Fritillaria imperialis*. *Cytologia*, **2**, 37–55.

Darlington, C. D., 1931 *a*, Meiosis in Diploid and Tetraploid *Primula sinensis*. *J. Genet.*, **24**, 65–96.

*Darlington, C. D., 1931 *b*, Cytological Theory in Relation to Heredity. *Nature*, **127**, 709–712.

*Darlington, C. D., 1931 *c*, Meiosis. *Biol. Revs.*, **6**, 221–264.

Darlington, C. D., 1931, *d*, The Cytological Theory of Inheritance in *Œnothera*. *J. Genet.*, **24**, 405–474.

Darlington, C. D., 1931 *e*, The Analysis of Chromosome Pairing in *Triticum* Hybrids. *Cytologia*, **3**, 21–25.

Darlington, C. D., 1932 *a*, The Control of the Chromosomes by the Genotype and its Bearing on some Evolutionary Problems. *Amer. Nat.*, **66**, 25–51.

*Darlington, C. D., 1932 *b*, *Chromosomes and Plant Breeding*. London (Macmillan).

Darlington, C. D., and Dark, S.O.S., 1932, The Origin and Behaviour of Chiasmata II. *Stenobothrus parallelus*. *Cytologia*, **3**, 169–185.

Darlington, C. D., and Janaki-Ammal, E. K., 1932, The Origin and Behaviour of Chiasmata I. Diploid and Tetraploid *Tulipa*. *Bot. Gaz.* (In the press.)

Darlington, C. D., and Mather, K., 1932, The Origin and Behaviour of Chiasmata III. Triploid *Tulipa*. *Cytologia*. (In the press.)

Darlington, C. D., and Moffett, A. A., 1930, Primary and Secondary Chromosome Balance in *Pyrus*. *J. Genet.*, **22**, 129–151.

See also : Buxton, Crane, Gairdner, Newton.

Davis, B. M., 1931, Some attempts to obtain haploids from *Œnothera Lamarckiana*. *Amer. Nat.*, **65**, 233–242.

Davis, B. M., and Kulkarni, C. G., 1930, The Cytology and Genetics of a Haploid Sport from *Œnothera franciscana*. *Genetics*, **15**, 55–80.

Dederer, P. H., 1928, Variations in chromosome number in the spermatogenesis of Phylosamia cynthia. *J. Morphol.*, **45**, 599–613.

Delaunay, L. N., 1925, The Chromosomes of Ornithogalum L. (English résumé). *Ann. Timiriasev Inst.*, **1**, (II, 3), 1–8.

Delaunay, L. N., 1926, Phylogenetische Chromosomenverkürzung. *Zeits. Zellforsch. u. mikr. Anat.*, **4**, 338–364.

Delaunay, L. N., 1929, Kern und Art. Typische Chromosomenformen. *Planta*, **7**, 100–112.

Delaunay, L. N., 1930, Rönthgenexperimente mit Weizen. *Wiss. Select. Inst. Kiew*, **6**, 3–34.

Dermen, H., 1931, Polyploidy in Petunia. *Amer. J. Bot.*, **18**, 250–261.

Detlefsen, J. A., and Clements, L. S., 1923, Genetic Variation in Linkage Values. *Proc. Nat. Acad. Sci.*, **9**, 149–156.

Digby, L., 1905, On the Cytology of Apogamy and Apospory. II. Preliminary Note on Apospory. *Proc. Roy. Soc.*, B **76**, 463–467.

Digby, L., 1912, The cytology of Primula kewensis and of other related Primula hybrids. *Ann. Bot.*, **26**, 357–388.

Digby, L., 1919, On the Archesporial and Meiotic Mitoses in *Osmunda*. *Ann. Bot.*, **33**, 135–172.

Dobell, C. C., 1925 *a*, The Life History and Chromosome Cycle of *Aggregata eberthi* (Protozoa, Sporozoa, Coccidia). *Parasitology*, **17**, 1–136.

Dobell, C. C., 1925 *b*, The chromosome cycle of the Sporozoa considered in relation to the Chromosome theory of heredity. *Cellule*, **35**, 167–192.

Dobzhansky, Th., 1929, Genetical and cytological proof of translocations involving the third and fourth chromosome of Drosophila melanogaster. *Biol. Zbl.*, **49**, 408–419.

Dobzhansky, Th., 1930 *a*, Translocations involving the third and fourth chromosomes of *Drosophila melanogaster*. *Genetics*, **15**, 347–399.

Dobzhansky, Th., 1930 *b*, Cytological map of the second chromosome of Drosophila melanogaster. *Biol. Zbl.*, **50**, 671–685.

Dobzhansky, Th., 1931 *a*, The decrease in crossing-over observed in translocations, and its probable explanation. *Amer. Nat.*, **65**, 214–232.

Dobzhansky, Th., 1931 *b*, Translocations involving the second and fourth chromosomes of Drosophila melanogaster. *Genetics*, **16**, 629–658.

Dobzhansky, Th., and Schultz, J., 1931, Evidence for multiple sex factors in the X-chromosome of Drosophila melanogaster. *Proc. Nat. Acad. Sci.*, **17**, 513–518.

DONCASTER, L., 1910, Gametogenesis of the Gall Fly, *Neuroterus lenticularis* (Spathegaster baccarum) I. *Proc. Roy. Soc.* B, **82,** 88–113.

DONCASTER, L., 1911, Gametogenesis of the Gall Fly, *Neuroterus lenticularis* II. *Proc. Roy. Soc.* B, **83,** 476–489.

DONCASTER, L., 1916, Gametogenesis and sex-determination of the gall-fly, *Neuroterus lenticularis* (Spathegaster baccarum) III. *Proc. Roy. Soc.* B, **89,** 183–200.

*DONCASTER, L., 1920, *An Introduction to the Study of Cytology.* Cambridge.

EARL, R. O., 1927, The nature of chromosomes. I. Effects of reagents on root-tip sections of *Vicia faba.* *Bot. Gaz.*, **84,** 58–74.

*EAST, E. M., 1929, The concept of the gene. *Proc. Int. Cong. Pl. Sc.*, **1,** 889–895.

EAST, E. M., 1930, The Production of Homozygotes through induced Parthenogenesis. *Science*, **72,** 148–149.

EISENTRAUT, M., 1926, Die spermatogonialen Teilungen bei Acridiern mit besonderer Berücksichtigung der Überkreuzungsfiguren. *Zeits. wiss. Zool.*, **127,** 141–183.

EISENTRAUT, M., 1928, Über das Auftreten von Chromosomenbläschen in den Reifeteilungen einiger Acridier. *Zeits. wiss. Zool.*, **128,** 253–266.

EKSTRAND, H., 1918, Zur Zytologie und Embryologie der Gattung Plantago (Vorläufige Mitteilung). *Svensk Bot. Tidsskr.*, **12,** 202–206.

EMERSON, S. H., 1924, The Absence of Chromosome Pairing during Meiosis in *Œnothera biennis.* *Pap. Mich. Acad. Sci. and Lett.*, **4,** 111–114.

EMERSON, S. H., 1929, The reduction division in a haploid Œnothera. *Cellule*, **39,** 159–165.

EMERSON, S. [H.], 1931, Parasynapsis and Apparent Chiasma Formation in *Œnothera.* *Amer. Nat.*, **65,** 551–555.

EMERSON, S. H., and BEADLE, G. W., 1930, A fertile tetraploid hybrid between *Euchlæna perennis* and *Zea Mays.* *Amer. Nat.*, **64,** 190–192.

EMERSON, S. H., and STURTEVANT, A. H., 1931, Genetic and Cytological Studies on Œnothera. III. The Translocation Interpretation. *Z.I.A.V.* **59,** 395–419.

EMME, H., 1928, Karyologie der Gattung *Secale* L. *Z.I.A.V.*, **47,** 99–124.

ERLANSON, E. W., 1929, Cytological conditions and evidences for hybridity in North American wild roses. *Bot. Gaz.*, **87,** 443–506.

ERLANSON, E. W., 1931 *a*, Sterility in wild roses and in some species hybrids. *Genetics*, **16,** 75–96.

ERLANSON, E. W., 1931 *b*, A Group of Tetraploid Roses in Central Oregon. *Bot. Gaz.*, **91,** 55–64.

ERLANSON, E. W., 1931 *c*, Chromosome Organisation in *Rosa.* *Cytologia*, **2,** 256–282.

*ERNST, A., 1918, *Bastardierung als Ursache der Apogamie im Pflanzenreich. Eine Hypothese zur experimentelle Vererbungs- und Abstammungslehre.* Jena.

EVANS, H. M., and SWEZY, O., 1928, A sex difference in chromosome lengths in the Mammalia. *Genetics*, **13,** 532–543.

EVANS, H. M., and SWEZY, O., 1929, The Chromosomes in Man: sex and somatic. *Mem. Univ. Calif.*, **9** (i), 1–41.

FARMER, J. B., and DIGBY, L., 1907, Studies in Apospory and Apogamy in Ferns. *Ann. Bot.*, **21,** 161–199.

FARMER, J. B., and MOORE, J. E. S., 1905, On the Maiotic Phase in Animals and Plants. *Quart. J. Micros. Sci.*, **48,** 489–557.

FASTEN, N., 1914, Spermatogenesis of the American crayfish, *Cambarus virilis* and *Cambarus immunis* (?) with special reference to synapsis and the chromatoid bodies. *J. Morphol.*, **25,** 587–649.

FASTEN, N., 1926, Spermatogenesis of the black-clawed crab, Lophopanopeus bellus (Stimpson) Rathbun. *Biol. Bull.*, **50,** 277–292.

FEDERLEY, H., 1912, Das Verhalten der Chromosomen bei der Spermatogenese der Schmetterlinge *Pygæra anachoreta, curtula* und *pigra* sowie einiger ihrer Bastarde. *Z.I.A.V.*, **9,** 1–110.

FEDERLEY, H., 1914, Ein Beitrag zur Kenntnis der Spermatogenese bei Mischlingen zwischen Eltern verschiedener systematischer Verwandtschaft. *Öfv. of Finsk Vetensk Soc. Förh.*, **56** (13), 1–28.

FEDERLEY, H., 1915, Chromosomenstudien an Mischlingen I. Die Chromosomenkonjugation bei der Gametogenese von Smerinthus populi. var. austauti × populi. *Öfv. of Finsk Vetensk Soc. Förh.*, **57** (26), 1–36. II. Die Spermatogenese des Bastards *Dicranura erminea* ♀ × *D. vinula* ♂ ibid. **57** (30), 1–26.

FEDERLEY, H., 1916, Chromosomenstudien an Mischlingen III. Die Spermatogenese des Bastards Chaerocampa porcellus ♀ × elpenor ♂. *Öfv. of Finsk Vetensk Soc. Förh.*, **58** (12), 1–17.

FEDERLEY, H., 1927, Ist die Chromosomenkonjugation eine conditio sina qua non für die Mendelspaltung ? *Hereditas*, **9,** 391–404.

FEDERLEY, H., 1931, Chromosomenanalyse der reziproken Bastarde zwischen Pygæra pigra und P. curtula sowie ihrer Ruckkreuzungsbastarde. *Zeits. Zellforsch. u. mikr. Anat.*, **12,** 772–816.

FERNANDES, A., 1931, Estudos nos Cromosomas das Liliáceas e Amarilidáceas. *Bol. Soc. Brot.* (Coimbra), **7,** 1–122.

FEULGEN, R., and IMHAÜSER, K., 1925, Über die für Nuklealreaktion und Nuklealfärbung verantwortlich zu machenden Gruppen nebst Bemerkungen zur Darstellung des Oxymethylfurfurols. II. *Zeits. f. physiol. Chem.*, **148,** 1–16.

FISK, E. L., 1931, The Chromosomes of Lathyrus tuberosus. *Proc. Nat. Acad. Sci.*, **17,** 511–513.

FOOT, K., and STROBELL, E. C., 1905, Prophases and metaphases of the first Maturation Spindle of *Allolobophora fœtida*. *Amer. J. Anat.*, **4,** 199–243.

FRANDSEN, H. N., and WINGE, Ø., 1932, *Brassica napocampestris,* a New Constant Amphidiploid Species Hybrid. *Hereditas*, **16,** 212–219.

FRASER, H. C. I., 1908, Contributions to the Cytology of Humaria rutilans, Fries. *Ann. Bot.*, **22,** 35–55.

FRIES, W., 1910, Die Entwicklung der Chromosomen im Ei von Branchipus Grub. und der parthenogenetischen Generationen von Artemia salina. *Arch. f. Zellforsch.*, **4,** 44–80.

FROLOWA, S., 1912, Idiochromosomen bei Ascaris megalocephala. *Arch f. Zellforsch.*, **9,** 149–167.

FROLOWA, S., 1926, Normale und polyploide Chromosomengarnituren bei einigen Drosophila-Arten. *Zeits. f. Zellforsch. u. mikr. Anat.*, **3,** 682–694.

FROST, H. B., 1925, Tetraploidy in Citrus. *Proc. Nat. Acad. Sci.*, **11,** 535–537.

FROST, H. B., 1927, Chromosome-Mutant Types in Stocks (*Matthiola incana* R. Br.). I. Characters due to Extra Chromosomes. *J. Hered.*, **18,** 474–486.

FROST, H. B., and MANN, M. C., 1924, Mutant forms of *Matthiola* resulting from non-disjunction. *Am. Nat.*, **58,** 569–572.

FRY, H. T., 1930, A critique of the cytological method : determining the structure of living cells from fixed ones. *Anat. Rec.*, **46,** 1–21.

Fukushima, E., 1929, Preliminary Report on Brassico-Raphanus Hybrids. *Proc. Imper. Acad.*, **5,** 48–50.

Fukushima, E., 1931, Formation of Diploid and Tetraploid Gametes in *Brassica*. *Jap. J. Bot.*, **5,** 273–283.

Gaines, E. F., and Aase, H. C., 1926, A haploid wheat plant. *Amer. J. Bot.*, **13,** 373–385.

Gairdner, A. E., 1926, *Campanula persicifolia* and its Tetraploid Form, " Telham Beauty." *J. Genet.*, **16,** 341–351.

Gairdner, A. E., and Darlington, C. D., 1931, Ring-Formation in Diploid and Polyploid *Campanula persicifolia*. *Genetica*, **13,** 113–150.

Gaiser, L. O., 1926 *a*, A list of chromosome numbers in Angiosperms. *Genetica*, **8,** 401–484.

Gaiser, L. O., 1926 *b*, Chromosome Numbers in Angiosperms, II. *Bibliogr. Genet*, **6,** 171–466.

Gates, R. R., 1907, Pollen development in hybrids of *Œnothera Lata* × *O. Lamarckiana*, and its relation to mutation. *Bot. Gaz.*, **43,** 81–115.

Gates, R. R., 1909, The stature and chromosomes of *Œnothera gigas*, de Vries. *Arch. f. Zellforsch.*, **3,** 525–552

Gates, R. R., 1924, Meiosis and Crossing-over. *J. Hered.*, **15,** 237–240.

Gates, R. R., 1928, The cytology of *Œnothera*. *Bibliogr. Genet.*, **4,** 401–492.

*Gates, R. R., 1931, The Cytological Basis of Mutations. *Amer. Nat.*, **65,** 97–120.

Gates, R. R., and Catcheside, D. G., 1931, Origin of Chromosome Linkage in *Œnothera*. *Nature*, **128,** 637.

Gates, R. R., and Goodwin, K. M., 1930, A new Haploid *Œnothera*, with some considerations on Haploidy in Plants and Animals. *J. Genet.*, **23,** 123–156.

Gates, R. R., and Goodwin, K. M., 1931, Meiosis in *Œnothera purpurata* and *Œ. blandina*. *Proc. Roy. Soc.* B, **109,** 149–164.

Gates, R. R., and Sheffield, F. M. L., 1929. Chromosome Linkage in certain *Œnothera* Hybrids. *Phil. Trans. R.S.* B, **217,** 367–394.

Geinitz, B., 1915, Über Abweichungen bei der Eireifung von Ascaris. *Arch. f. Zellforsch.*, **13,** 588–633.

Geitler, L., 1927, Somatische Teilung, Reduktionsteilung, Copulation und Parthenogenese bei *Cocconeis placentula*. *Arch. Prot.*, **59,** 506–549.

Geitler, L., 1929, Zur Zytologie von *Ephedra*. *Österr. Bot. Zeits.*, **78,** 242–250.

Gelei, J., 1921, Weitere Studien über die Oogenese des *Dendrocœlum lacteum*. II. Die Längskonjugation der Chromosomen. *Arch. f. Zellforsch.*, **16,** 88–169.

Gelei, J., 1922, Weitere Studien über die Oogenese des *Dendrocœlum lacteum*. III. Die Konjugationsfrage der Chromosomen in der Literatur und meine Befunde. *Arch. f. Zellforsch.*, **16,** 299–370.

*Goldschmidt, R., 1928, The Gene. *Quart. Rev. Biol.*, **3,** 307–324.

*Goldschmidt, R., 1929, Geschlechtsbestimmung im Tier- und Pflanzenreich. *Biol. Zbl.*, **49,** 641–648.

*Goldschmidt, R., 1931, Analysis of Intersexuality in the Gipsy Moth. *Quart. Rev. Biol.*, **6,** 125–142.

Goodspeed, T. H., 1929, Cytological and other features of variant plants produced from X-rayed sex cells of *Nicotiana tabacum*. *Bot. Gaz.*, **87,** 563–582.

Goodspeed, T. H., 1930, Occurrence of Triploid and Tetraploid Individuals in X-ray Progenies of Nicotiana Tabacum. *Univ. Calif. Pub. Bot.*, **11,** 299–308.

Goodspeed, T. H., and Avery, P., 1929 *a*, The occurrence of chromosome variants in Nicotiana alata Lk. et Otto. *Proc. Nat. Acad. Sci.*, **15,** 343–345.

Goodspeed, T. H., and Avery, P., 1929 *b*, The occurrence of a *Nicotiana glutinosa* haplont. *Proc. Nat. Acad. Sci.*, **15,** 502–504.

Goodspeed, T. H., and Avery, P., 1930, Nature and Significance of Structural Chromosome Alterations Induced by X-rays and Radium. *Cytologia*, **1,** 308–327.

Goodspeed, T. H., and Clausen, R. E., 1927 *a*, Interspecific Hybridization in Nicotiana V. Cytological features of the two F_1 hybrids made with Nicotiana bigelovii as a parent. *Univ. Calif. Pub. Bot.*, **11,** 117–125.

Goodspeed, T. H., and Clausen, R. E., 1927 *b*, Interspecific Hybridization in Nicotiana VI. Cytological features of sylvestris-tabacum hybrids. *Univ. Cal. Pub. Bot.*, **11,** 127–140.

Goodspeed, T. H., Clausen, R. E., and Chipman, R. H., 1926, Interspecific Hybridization in Nicotiana IV. Some Cytological Features of the paniculata-rustica hybrid and its Derivatives. *Univ. Calif. Pub. Bot.*, **11,** 103–116.

Gotoh, K., 1924. Über die Chromosomenzahl von *Secale cereale*, L. *Bot. Mag. Tokyo*, **38,** 135–152.

Gowen, J. W., 1928, On the Mechanism of Chromosome Behavior in Male and Female Drosophila. *Proc. Nat. Acad. Sci.*, **14,** 475–477.

Gowen, J. W., 1929, The Cell Division at which Crossing Over takes Place. *Proc. Nat. Acad. Sci.*, **15,** 266–268.

Gowen, M. S., and Gowen, J. W., 1922, Complete linkage in *Drosophila melanogaster*. *Amer. Nat.*, **56,** 286–288.

Granata, L., 1910, Le cinesi spermatogenetiche di Pamphagus marmoratus (Burm.). *Arch. f. Zellforsch*, **5,** 182–214.

Graubard, M. A., 1932, Inversion in *Drosophila melanogaster*. *Genetics* **17,** 81–105.

Gray, J., 1931, *Experimental Cytology*, Cambridge.

Grégoire, V., 1905, Les résultats acquis sur les cinèses de maturation dans les deux règnes. (Premier mémoire.) Revue critique de la littérature. *Cellule* **22,** 219–376.

Grégoire, V., 1909, La réduction dans le Zoögonus mirus Lss. et le " Primärtypus." *Cellule*, **25,** 243–287.

Grégoire, V., 1910, Les cinèses de maturation dans les deux règnes. L'unité essentielle du processus méiotique. (Second mémoire.) *Cellule*, **26,** 221–422.

Grégoire, V., 1931, Euchromocentres et chromosomes dans les végétaux. Acad. Roy. Belg., Bull. classe de Sci. (5) 17, 1435–1448.

Gregor, J. W., and Sansome, F. W., 1930, Experiments on the Genetics of Wild Populations. II. *Phleum pratense* L. and the hybrid *P. pratense* L. × *P. alpinum* L. *J. Genet.*, **22,** 373–387.

Gurwitsch, A., 1926, Das Problem der Zellteilung physiologisch betrachtet. *Monog. a.d. Gesamtgebiet d. physiol. d. Pfl. u. d. Tiere*, **11,** Berlin.

Gustafsson, A., 1930, Kastrierungen und Pseudogamie bei Rubus. *Bot. Not.* (Lund), 1930, 477–494.

Gustafsson, A., 1931, Sind die Canina-Rosen apomiktisch ? *Bot. Not.* (Lund), 1931, 21–30.

Gustafsson, A., 1932, Zytologische und experimentelle Studien in der Gattung *Taraxacum*. *Hereditas*, **16,** 41–62.

Gwynne-Vaughan, H. C. I., and Williamson, H. S., 1931, Contributions to the study of Pyronema confluens. *Ann. Bot.*, **45,** 355–371.

HAASE-BESSELL, G., 1916, Digitalisstudien I. *Z.I.A.V.*, **16,** 293–314.

HAASE-BESSELL, G., 1922, Digitalisstudien II. *Z.I.A.V.*, **27,** 1–26.

HAASE-BESSELL, G., 1926, Digitalisstudien III. *Z.I.A.V.*, **42,** 1–46.

HABERLANDT, G., 1921 *a*, Über experimentelle Erzeugung von Adventivembryonen bei Œnothera Lamarckiana. *Sitzb. preuss. Akad. Wiss.*, **40,** 695–725.

HABERLANDT, G., 1921 *b*, Die Entwicklungserregung der Eizellen einiger parthenogenetischer Kompositen. *Sitzb. preuss. Akad. Wiss.*, **51,** 861–881.

HABERLANDT, G., 1923, Zur Embryologie von Allium odorum L. *Ber. Deuts. Bot. Ges.*, **41,** 174–179.

HABERLANDT, G., 1927, Zur Cytologie und Physiologie des weiblichen Gametophyten von Œnothera. *Sitzb. preuss. Akad. Wiss.*, **7,** 33–47.

HÄCKER, V., 1892, Die heterotypische Kernteilung im Cyklus der generativen Zellen. *Ber. Naturf. Ges. Freib.*, **6,** 160–193.

HAGERUP, O., 1927, *Empetrum Hermaphroditum* (Lge) Hagerup, A new tetraploid bisexual Species. *Dansk Bot. Ark.*, **5** (2), 1–17.

HAGERUP, O., 1932, Über Polyploidie in Beziehung zu Klima, Ökologie und Phylogenie. Chromosomenzahlen aus Timbuktu. *Hereditas*, **16,** 19–40.

HÅKANSSON, A., 1925, Zur Zytologie der Gattung *Godetia*. *Hereditas*, **6,** 257–274.

HÅKANSSON, A., 1926, Über das Verhalten der Chromosomen bei der heterotypischen Teilung schwedischer *Œnothera Lamarckiana* und einiger ihrer Mutanten und Bastarde. *Hereditas*, **8,** 255–304.

HÅKANSSON, A., 1928, Die Reduktionsteilung in den Samenanlagen einiger Œnotheren. *Hereditas*, **11,** 129–181.

HÅKANSSON, A., 1929 *a*, Chromosomenringe in *Pisum* und ihre mutmassliche genetische Bedeutung. *Hereditas*, **12,** 1–10.

HÅKANSSON, A., 1929 *b*, Die Chromosomen in der Kreuzung *Salix viminalis* × *caprea* von Heribert-Nilsson. *Hereditas*, **13,** 1–52.

HÅKANSSON, A., 1929 *c*, Über verschiedene Chromosomenzahlen in *Scirpus palustris* L. *Hereditas*, **13,** 53–60.

HÅKANSSON, A., 1930 *a*, Die Chromosomenreduktion bei einigen Mutanten und Bastarden von *Œnothera Lamarckiana*. *Jahrb. Wiss. Bot.*, **72,** 385–402.

HÅKANSSON, A., 1930 *b*, Zur Zytologie trisomischer Mutanten aus *Œnothera Lamarckiana*. *Hereditas*, **14,** 1–32.

HÅKANSSON, A., 1931 *a*, Über Chromosomenverkettung in *Pisum*. *Hereditas*, **15,** 17–61.

HÅKANSSON, A., 1931 *b*, Chromosomenverkettung bei Godetia und Clarkia. *Ber. Deuts. Bot. Ges.*, **49,** 228–234.

HALDANE, J. B. S., 1919, The Combination of Linkage Values and the Calculation of Distances between the Loci of Linked Factors. *J. Genet.*, **8,** 291–297.

HALDANE, J. B. S., 1922, Sex Ratio and Unisexual Sterility in Hybrid Animals. *J. Genet.*, **12,** 101–109.

*HALDANE, J. B. S., 1927, The comparative genetics of colour in rodents and carnivora. *Biol. Rev.*, **2,** 199–212.

*HALDANE, J. B. S., 1929, The Species Problem in the Light of Genetics. *Nature*, **124,** 514–516.

HALDANE, J. B. S., 1930, Theoretical Genetics of Autopolyploids. *J. Genet.*, **22,** 359–372.

HALDANE, J. B. S., 1931, The Cytological Basis of Genetical Interference. *Cytologia*, **3,** 54–65.

HALDANE, J. B. S., 1932 *a*, The Time of Action of Genes and its bearing on some Evolutionary Problems. *Amer. Nat.*, **46,** 5–24.

HALDANE, J. B. S., 1932 *b*, Biochemical Aspects of Genetics. *Biol. Revs.* (In the Press.)

HALDANE, J. B. S., 1932 *c*, *The Causes of Evolution.* London (Longmans, Green & Co.).

HANCE, R. T., 1927, Parental chromosome dimensions in Ascaris. A study of the effect of cellular environment on chromosome size. *J. Morphol.*, **44,** 117–125.

HARMAN, M. T., 1920, Chromosome studies in Tettigidæ. II. Chromosomes of Paratettix BB and CC and their Hybrid BC. *Biol. Bull.*, **38,** 213–230.

HARRISON, J. W. H., 1920 *a*, Genetical studies in the moths of the Geometrid genus *Oporabia* (*Oporinia*) with a special consideration of Melanism in the Lepidoptera. *J. Genet.*, **9,** 195–280.

HARRISON, J. W. H., 1920 *b*, The inheritance of melanism in the genus *Tephrosia* (*Ectropis*) with some consideration of the Inconstancy of Unit Characters under Crossing. *J. Genet.*, **10,** 61–86.

HARRISON, J. W. H., and DONCASTER, L., 1914, On hybrids between moths of the Geometrid family *Bistoninæ*, with an Account of the Behaviour of the Chromosomes in Gametogenesis in *Lycia* (*Biston*) *Hirtaria*, *Ithysia* (*Nyssa*) *Zonaria* and their Hybrids. *J. Genet.*, **3,** 229–248.

*HARTMANN, M., 1929 *a*, Fortpflanzung und Befruchtung als Grundlage der Vererbung. *Handb. d. Vererbungswiss.*, **1.**

*HARTMANN, M., 1929 *b*, Verteilung, Bestimmung und Vererbung des Geschlechtes bei den Protisten und Thallophyten. *Handb. d. Vererbungswiss.*, **2.**

HAYDEN, M. A., 1925, Karyosphere Formation and Synapsis in the Beetle Phanæus. *J. Morphol.*, **40,** 261–297.

HEDAYETULLAH, S., 1931, On the Structure and Division of the Somatic Chromosomes in *Narcissus*. *J. Roy. Micr. Soc.*, **51,** 347–386.

*HEGNER, R. W., 1914, *The Germ Cell Cycle in Animals.* New York.

HEILBORN, O., 1927, Chromosome Numbers in *Draba*. *Hereditas*, **9,** 59–68.

*HEILBRUNN, L. V., 1928, *The Colloid Chemistry of Protoplasm.* Berlin.

HEIMANS, J., 1928, Chromosomen und Befruchtung bei Lilium Martagon. *Rec. Trav. Bot. Néerl.*, **25A,** 138–167.

HEITZ, E., 1926, Der Nachweis der Chromosomen : Vergleichende Studien über ihre Zahl, Grösse und Form im Pflanzenreich, I. *Zeits. f. Bot.*, **18,** 625–681.

HEITZ, E., 1928, Das Heterochromatin der Moose. I. *Jahrb. wiss. Bot.*, **69,** 762–818.

HEITZ, E., 1929, Heterochromatin, Chromocentren, Chromomeren. *Der Deuts. Bot. Ges.*, **47,** 274–284.

HELMS, A., and JØRGENSEN, C. A., 1925, Maglemose i Grib Skov. VIII. Birkene paa Maglemose. *Dansk Bot. Tidsskr.*, **39,** 57–135.

HELWIG, E. R., 1929, Chromosomal variations correlated with geographic distribution in Circotettix verruculatus (Orthoptera). *J. Morphol.*, **47,** 1–36.

HENKING, H., 1890, Untersuchungen über die ersten Entwicklungsvorgänge in den Eiern der Insekten. 2. Über Spermatogenese und deren Beziegung zur Eientwicklung bei Pyrrhocoris apterus, L. *Zeits. wiss. Zool.*, **51,** 685–736.

*HERTWIG, O., 1917, Documente zur Geschichte der Zeugungslehre, etc. *Arch. mikr. Anat.*, **90,** Abt. II, 1–168.

HERTWIG, P., 1920, Abweichende Form der Parthenogenese bei einer Mutation von Rhabditis pellio, eine experimentell cytologische Untersuchung. *Arch. mikr. Anat.*, **94,** 303–337.

*HERTWIG, P., 1927, Vererbungslehre. *Tab. Biol.*, **4,** 114–215.

Higgins, E. M., 1930, Reduction Division in a Species of *Cladophora*. *Ann. Bot.*, **44,** 587–592.

Hirayanagi, H., 1929, Chromosome Arrangement III. The Pollen Mother Cells of the Vine. *Mem. Coll. Sci. Kyoto,* B **4,** 273–281.

Hoar, C. S., 1931, Meiosis in Hypericum punctatum Lam. *Bot. Gaz.*, **92,** 396–406.

Hœppener, E. and Renner, O., 1929. Genetische und Zytologische Œnotherenstudien II. *Bot. Abh.* (Goebel), **15,** 1–86.

Hogben, L. T., 1920, Studies on Synapsis I and II. I. Oogenesis in the Hymenoptera ; II. Parallel Conjugation and the Prophase Complex in Periplaneta, with Special Reference to the Pre-Meiotic Telophase. *Proc. Roy. Soc.*, B **91,** 268–292, 305–329.

Hollingshead, L., 1928 *a*. A preliminary note on the occurrence of haploids in *Crepis*. *Amer. Nat.*, **62,** 282–284.

Hollingshead, L., 1928 *b*. Chimaeras in Crepis. *Univ. Calif. Pub. Agr. Sci.*, **2,** 343–354.

Hollingshead, L., 1930 *a*, A Cytological Study of Haploid Crepis Capillaris Plants. *Univ. Calif. Pub. Agr. Sci.*, **6,** 107–134.

Hollingshead, L., 1930 *b*, Cytological Investigations of Hybrids and Hybrid Derivatives of Crepis capillaris and Crepis tectorum. *Univ. Calif. Pub. Agr. Sci.*, **6,** 55–94.

Hollingshead, L., 1932, The occurrence of unpaired chromosomes in hybrids between varieties of *Triticum vulgare*. *Cytologia*, **3,** 119–141.

Hollingshead, L. and Babcock, E. B., 1930, Chromosomes and Phylogeny in Crepis. *Univ. Calif. Pub. Agr. Sci.*, **6,** 1–53.

Holmgren, I., 1919, Zytologische Studien über die Fortpflanzung bei den Gattungen Erigeron und Eupatorium. *K. Sv. Vet. Akad. Handl.*, **59** (7), 1–118.

Honing, J. A., 1928, Canna crosses II. The chromosome number of Canna glauca, C. glauca × C. indica F_1, C. aureo-vittata and C. aureo-vittata gigas. *Med. Landbouwhoogesch. Wageningen*, **32,** 1–14.

Huettner, A. F., 1930, The spermatogenesis of Drosophila melanogaster. *Zeits. Zellforsch. u. mikr. Anat.*, **11,** 615–637.

Hughes-Schrader, S., 1927, Origin and Differentiation of the male and female germ-cells in the hermaphrodite of Icerya purchasi (Coccidæ). *Zeits. f. Zellforsch. u. mikr. Anat.*, **6,** 509–540. (*See also :* Schrader.)

Hughes-Schrader, S., 1930, The cytology of several species of iceryine coccids, with special reference to parthenogenesis and haploidy. *J. Morphol.*, **50,** 475–495.

Hughes-Schrader, S., 1931, A study of the chromosome cycle and the meiotic division figure in Llaveia bouvari—a primitive coccid. *Zeits. Zellforsch. u. mikr. Anat.*, **13,** 742–769.

Hurst, C. C., 1931, Embryo-sac Formation in Diploid and Polyploid Species of Roseæ. *Proc. Roy. Soc.*, B **109,** 126–148.

Huskins, C. L., 1927, On the Genetics and Cytology of Fatuoid or False Wild Oats. *J. Genet.*, **18,** 315–364

Huskins, C. L., 1928, On the Cytology of Speltoid Wheats in relation to their Origin and Genetic Behaviour. *J. Genet.*, **20,** 103–122.

Huskins, C. L., 1931 *a*, The Origin of Spartina Townsendii. *Genetica*, **12,** 531–538.

Huskins, C. L., 1931 *b*, A cytological Study of Vilmorin's Unfixable Dwarf Wheat. *J. Genet.*, **25,** 113–124.

Huskins, C. L., and Smith, S. G., 1932, A Cytological Study of the Genus *Sorghum* Pers., I. The Somatic Chromosomes. *J. Genet.*, **25,** 241–249.

ICHIJIMA, K., 1926, Cytological and Genetic Studies on Fragaria. *Genetics*, **11**, 590–604.

ICHIJIMA, K., 1930, Studies on the Genetics of *Fragaria*. *Z.I.A.V.*, **55**, 300–347.

INARIYAMA, S., 1928, On the Spiral Structure of Chromosomes in *Hosta Sieboldiana* Engl. *Bot. Mag. Tokyo*, **42**, 486–489 (Japanese).

ISHIKAWA, M., 1911, Cytologische Studien von Dahlien, *Bot. Mag. Tokyo*, **25**, 1–8.

ISHIKAWA, M., 1918, Studies on the Embryo-Sac and Fertilisation in Œnothera. *Ann. Bot.*, **32**, 279–317.

JANSSENS, F. A., 1909, Spermatogénèse dans les Batraciens V., La Théorie de la Chiasmatypie, Nouvelle interpretation des cinèses de maturation. *Cellule*, **25**, 387–411.

JANSSENS, F. A., 1924, La Chiasmatypie dans les Insectes. *Cellule*, **34**, 135–359.

JARETSKY, R., 1928, Histologische und karyologische Studien an Polygonaceen. *Jahrb. wiss. Bot.*, **69**, 357–490.

JARETSKY, R., 1930, Zur Zytologie der Fagales. *Planta*, **10**, 120–137.

JENKINS, J. A., 1929, Chromosome homologies in wheat and *Ægilops*. *Amer. J. Bot.*, **16**, 238–245.

JENNINGS, H. S., 1923, The numerical relations in the crossing-over of the genes, with a critical examination of the theory that the genes are arranged in a linear series. *Genetics*, **8**, 390–457.

JOHANNSEN, W., 1911, The Genotype Conception of Heredity, *Amer. Nat.*, **45**, 129–159.

JOHANNSEN, W., 1923, Some remarks about units in heredity. *Hereditas*, **4**, 133–141.

JØRGENSEN, C. A., 1923, Studies on Callitrichaceæ. *Dansk Bot. Tidsskr.*, **38**, 81–126

JØRGENSEN, C. A., 1927, Cytological and Experimental Studies in the Genus *Lamium*. *Hereditas*, **9**, 126–136.

JØRGENSEN, C. A., 1928, The Experimental Formation of Heteroploid Plants in the Genus *Solanum*. *J. Genet.*, **19**, 133–211.

JUEL, H. O., 1900, Vergleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei der Gattung *Antennaria*. *K. Sv. Vet. Akad. Handl.*, **33** (5), 1–59.

JUEL, H. O., 1905, Die Tetradenteilung bei Taraxacum und anderen Cichorieen. *K. Sv. Vet. Akad. Handl.*, **39** (4), 1–21.

JUNKER, H., 1923, Cytologische Untersuchungen an den Geschlechtsorganen der halbzwittrigen Steinfliege *Perla marginata* (Panzer). *Arch. f. Zellforsch.*, **17**, 185–259.

KACHIDZE, N., 1929, Karyologische Studien über die Familie Dipsacaceæ. *Planta*, **7**, 482–502.

KAGAWA, F., 1928, Cytological Studies on *Triticum* and *Ægilops* II. On the genus crosses between *Triticum* and *Ægilops*. *Jap. J. Bot.*, **4**, 1–26.

KAGAWA, F., 1929 *a*, On the Phylogeny of some Cereals and Related Plants as Considered from the Size and Shape of Chromosomes. *Jap. J. Bot.*, **4**, 363–383.

KAGAWA, F., 1929 *b*, Cytological Studies on the pollen-formation of the hybrids between *Triticum* and *Ægilops*. *Jap. J. Bot.*, **4**, 345–361.

KAGAWA, F., 1931, Chromosome Studies of a Species Cross in *Ægilops*. *Bull. Utsunomiya Ag. Coll.*, **1**, 57–60.

KAHLE, W., 1908, Die Pædogenese des Cecidomyiden. *Zoologica* (Stuttgart), **21** (55), 1–80.

KARLING, J. S., 1928, Nuclear and cell division in the antheridial filaments of the Characeæ. *Bull. Torrey Bot. Club*, **55**, 11–39.

KARPECHENKO, G. D., 1927 *a*, The Production of Polyploid Gametes in Hybrids. *Hereditas*, **9**, 349–368.

KARPECHENKO, G. D., 1927 *b*, Polyploid hybrids of Raphanus sativus L. × Brassica oleracea L. (English summary). *Bull. Appl. Bot.*, **17** (3), 305–410.

KARPECHENKO, G. D., 1928, Polyploid Hybrids of *Raphanus sativus* L. × *Brassica oleracea* L. *Z.I.A.V.*, **48**, 1–85.

KARPECHENKO, G. D., 1929, A contribution to the synthesis of a constant hybrid of three species (English summary). *Proc. U.S.S.R. Cong. Genet.*, **2**, 277–294.

KARPECHENKO, G. D., and SHCHAVINSKAIA, S. A., 1929, On sexual incompatibility of tetraploid hybrids. *Proc. U.S.R.R. Cong. Genet.*, **2**, 267–276. (English summary.)

KATER, J. MCA., 1926, Chromosomal vesicles and the structure of the resting nucleus in *Phaseolus*. *Biol. Bull.*, **51**, 209–224.

KATTERMANN, G., 1930, Chromosomenuntersuchungen bei Gramineen. *Planta*, **12**, 19–37.

KATTERMANN, G., 1931, Über die Bildung polyvalenter Chromosomenverbände bei einigen Gramineen. *Planta*, **12**, 732–744.

KAUFMANN, B. P., 1926 *a*, Chromosome structure and its relation to the chromosome cycle I. Somatic mitoses in *Tradescantia pilosa* Lehm. *Amer. J. Bot.*, **13**, 59–80.

KAUFMANN, B. P., 1926 *b*, Chromosome structure and its relation to the chromosome cycle II. *Podophyllum peltatum*. *Amer. J. Bot.*, **13**, 355–363.

KAUFMANN, B. P., 1931, Chromonemata in somatic and meiotic mitoses. *Amer. Nat.*, **65**, 280–283.

KAWAGUCHI, E., 1928, Zytologische Untersuchungen am Seidenspinner und seinen Verwandten I. Gametogenese von Bombyx mori L. und B. mandarina M. und ihre Bastarde. *Zeits. f. Zellforsch. u. mikr. Anat.*, **7**, 519–552.

KAWAKAMI, J., 1930, Chromosome numbers in Leguminosæ. *Bot. Mag. Tokyo*, **44**, 319–328.

KEUNEKE, W., 1924, Über die Spermatogenese einiger Dipteren. *Zeits. Zell. u. Geweb.*, **1**, 357–412.

KIHARA, H., 1919, Über cytologische Studien bei einigen Getreidearten I. and II. I. Spezies-Bastarde des Weizens und Weizenroggen-Bastard. II. Chromosomenzahlen und Verwandtschaftsverhaltnisse unter Avena-Arten. *Bot. Mag. Tokyo*, **33**, 17–38, 94–97.

KIHARA, H., 1921, Über cytologische Studien bei einigen Getreidearten. III. *Bot. Mag. Tokyo*, **35**, 19–44.

KIHARA, H., 1924, Cytologische und Genetische Studien bei wichtigen Getreidearten, etc. *Mem. Coll. Sci. Kyoto*, **1**, 1–200.

KIHARA, H., 1927 *a*, Über das Verhalten der "end-to-end" gebundenen Chromosomen von Rumex acetosella und Œnothera biennis wahrend der heterotypischen Kernteilung. Beitrag zur Frage der Para- und Metasyndese. *Jahrb. wiss. Bot.*, **66**, 429–460.

KIHARA, H., 1927 *b*, Über die Vorbehandlung einiger pflanzlicher Objecte bei der Fixierung der Pollenmutterzellen. *Bot. Mag. Tokyo*, **41**, 124–128.

KIHARA, H., 1929 *a*, The Sex chromosomes of *Humulus japonicus*. *Jap. J. Genet.*, **4**, 55–63.

KIHARA, H., 1929 *b*, A case of linkage of sex chromosomes with autosomes in the pollen mother cell of *Humulus japonicus* (English summary). *Jap. J. Genet.*, **5,** 73–80.

KIHARA, H., 1929 *c*, Conjugation of homologous chromosomes in the genus hybrids *Triticum* × *Ægilops* and species hybrids of *Ægilops*. *Cytologia*, **1**, 1–15.

KIHARA, H., 1930 *a*, Karyologische Studien an *Fragaria* mit besonderer Berücksichtigung der Geschlechtschromosomen. *Cytologia*, **1,** 345–375.

KIHARA, H., 1930 *b*, Genomanalyse bei *Triticum* und *Ægilops* I. KIHARA, H., and NISHIYAMA, I., 1930, Genomaffinitäten in tri-tetra und pentaploiden Weizenbastarden. *Cytologia*, **1,** 263–284.

KIHARA, H., 1931 *a*, Genomanalyse bei *Triticum* und *Ægilops* II. *Ægilotricum* und *Ægilops cylindrica*. *Cytologia*, **2,** 106–156.

KIHARA, H., 1931, Genomanalyse bei *Triticum* und *Ægilops* III. KIHARA, H., and KATAYAMA, Y., 1931, Zur Entstehungsweise eines neuen konstanten oktoploiden *Ægilotricum*. Cytologia, **2,** 234–255.

KIHARA, H., and ONO, T., 1925, The Sex-Chromosomes of *Rumex Acetosa*. *Z.I.A.V.*, **39,** 1–7.

KIHARA, H., and ONO, T., 1926, Chromosomenzahlen und systematische Gruppierung der Rumex-Arten. *Zeits. f. Zellforsch. u. mikr. Anat.*, **4,** 475–481.

KIHARA, H., and YAMAMOTO, Y., 1931, Karyomorphologische Untersuchungen an *Rumex acetosa* L. und *Rumex montanus* Desf. *Cytologia*, **3,** 84–118.

KIRSSANOW, B. A., 1931, Über die Nachwirkung verschiedener Temperaturen und der X-Strahlen auf das Crossing-over im dritten Chromosom bei Drosophila melanogaster. *Biol. Zbl.*, **51,** 529–533.

*KNIEP, H., 1928, *Die Sexualität der niederen Pflanzen*. Jena.

*KNIEP, H., 1929, Vererbungserscheinungen bei Pilzen. *Bibliogr. Genet.*, **5,** 371–478.

KOBEL, F., 1927, Zytologische Untersuchungen an Prunoideen und Pomoideen. *Arch. Jul.-Klaus-Stift.*, **3,** 1–84.

KOLLER, P. C., 1932 *a*, The relation of fertility factors to crossing-over reduction in the *Drosophila obscura* hybrid. *Z.I.A.V.*, **60,** 137–151.

KOLLER, P. C., 1932 *b*, Constitution of the X-Chromosome in *Drosophila obscura*. *Nature*, **129,** 616.

KORNHAUSER, S. I., 1914, A comparative study of the chromosomes in the spermatogenesis of Enchenopa binotata (Say) and Enchenopa (Campylenchia Stål) curvata (Fabr). *Arch. f. Zellforsch.*, **12,** 241–298.

KOSTOFF, D., 1929, An androgenic Nicotiana haploid. *Zeits. f. Zellforsch. u. mikr. Anat.*, **9,** 640–642.

KRAUSE, O., 1931, Zytologische Studien bei den Urticales unter besonderer Berücksichtigung der Gattung Dorstenia. *Planta*, **13,** 29–84.

KUHN, E., 1929 *a*, Die Beziehung der Chromocentren zur Chromosomenbildung. *Ber. Deuts. Bot. Ges.*, **47,** 421–430.

KUHN, E., 1929 *b*, Ein Beweis für die Lebensfähigkeit von Spermatozoen ohne X- und Y-Chromosom bei *Drosophila melanogaster*. *Z.I.A.V.*, **53,** 26–37.

*KUHN, E., 1930, Pseudogamie und Androgenesis bei Pflanzen. *Züchter*, **2,** 124–136.

KULKARNI, C. G., 1929, Meiosis in Pollen Mother Cells of Strains of Œnothera pratincola Bartlett. *Bot. Gaz.*, **87,** 218–259.

KUNIEDA, H., 1926, On the Mitosis and Fertilisation of *Sargassum Horneri* Ag. *Bot. Mag. Tokyo*, **40,** 545–550.

KUWADA, Y., 1910, A Cytological Study of *Oryza sativa* L. *Bot. Mag. Tokyo*, **24,** 267–281.

KUWADA, Y., 1921, On the So-called Longitudinal Split of Chromosomes in the Telophase. *Bot. Mag. Tokyo*, **35,** 99–105.

KUWADA, Y., 1926, On the Structure of the Anaphasic Chromosomes in the Somatic Mitoses in *Vicia Faba*, with Special Reference to the So-called Longitudinal Split of Chromosomes in the Telophase. *Mem. Coll. Sci. Kyoto* B., **2,** 1–13.

KUWADA, Y., 1927, On the Spiral Structure of Chromosomes. *Bot. Mag. Tokyo*, **41,** 100–109.

KUWADA, Y., 1928, An Occurrence of Restitution-Nuclei in the Formation of the Embryo sacs in *Balanophora japonica*, Mak. *Bot. Mag. Tokyo*, **42,** 117–129.

KUWADA, Y., 1929, Chromosome Arrangement I. Model Experiments with Floating Magnets and some Theoretical Considerations on the Problem. *Mem. Coll. Sci. Kyoto*, **4,** 199–264.

KUWADA, Y., and SAKAMURA, T., 1926, A contribution to the Colloidchemical and Morphological Study of Chromosomes. *Protoplasma*, **1,** 239–254.

KUWADA, Y., and SUGIMOTO, T., 1926, On the Structure of the Chromosomes in *Tradescantia virginica*. *Bot. Mag. Tokyo*, **40,** 19–20.

KUWADA, Y., and SUGIMOTO, T., 1928, On the Staining Reactions of Chromosomes. *Protoplasma*, **3,** 531–535.

LA-COUR, L., 1931, Improvements in Everyday Technique in Plant Cytology. *J. Roy. Micr. Sci.*, **51,** 119–126.

LAMMERTS, W. E., 1929, Interspecific Hybridization in Nicotiana IX. Further Studies of the Cytology of the Backcross progenies of the *Paniculata-Rustica* hybrid. *Genetics*, **14,** 286–304.

LAMMERTS, W. E., 1931, Interspecific Hybridization in Nicotiana XII. The Amphidiploid *rustica-paniculata* hybrid ; its origin and cyto-genetic behavior. *Genetics*, **16,** 191–211.

LANCEFIELD, D. E., 1929, A genetic study of two races or physiological species of *Drosophila obscura*. *Z.I.A.V.*, **52,** 287–317.

LANCEFIELD, R. C., and METZ, C. W., 1922, The sex-linked group of mutant characters in Drosophila Willistoni. *Amer. Nat.*, **56,** 211–241.

LANGLET, O. F. I., 1927, Beiträge zur Zytologie der Ranunculazeen. *Sv. Bot. Tidsskr.*, **21,** 1–17.

LANGLET, O. F. I., and SÖDERBERG, E., 1929, Über die Chromosomenzahlen einiger Nymphaeaceen. *Acta Hort. Berg.*, **9,** 85–104.

LAWRENCE, W. J. C., 1929, The Genetics and Cytology of Dahlia species. *J. Genet.*, **21,** 125–159.

LAWRENCE, W. J. C., 1931 *a*, The Genetics and Cytology of *Dahlia variabilis*. *J. Genet.*, **24,** 257–306.

LAWRENCE, W. J. C., 1931 *b*, Mutation or Segregation in the Octoploid *Dahlia variabilis ?* *J. Genet.*, **24,** 307–324.

LAWRENCE, W. J. C., 1931 *c*, The Secondary Association of Chromosomes. *Cytologia*, **2,** 352–384.

LAWRENCE, W. J. C., 1931 *d*, The Chromosome Constitution of *Cardamine pratensis* and *Verbascum phœniceum*. *Genetica*, **13,** 183–208. (*See also :* Crane.)

LEAGUE, B. B., 1928, The chromosomes of the guinea pig. *J. Morphol.*, **46,** 131–142.

LEBEDEFF, V. N., 1932, The New Phenomenon in Wheat-Rye Hybrids. (Plant Breeding Inst., Belaya Zerkov, Ukraine.) Kiev.

LEBRUN, H., 1902, La cytodiérèse de l'œuf. La vésicule germinative et les globules polaires chez les Anoures. *Cellule*, **19,** 315–402.

LESLEY, J. W., 1928, The cytological and genetical study of progenies in triploid tomatoes. *Genetics*, **13**, 1–43.

LESLEY, J. W., and LESLEY, M. M., 1929, Chromosome fragmentation and mutation in tomato. *Genetics*, **14**, 321–336.

LESLEY, M. M., 1926, Maturation in diploid and triploid Tomatoes. *Genetics*, **11**, 267–279.

LESLEY, M. M., and FROST, H. B., 1927, Mendelian Inheritance of Chromosome Shape in *Matthiola*. *Genetics*, **12**, 449–460.

LESLEY, M. M., and FROST, H. B., 1928, Two extreme " small " Matthiola plants ; a haploid with one and a diploid with two additional chromosome fragments. *Amer. Nat.*, **62**, 22–33.

LESLEY, M. M., and LESLEY, J. W., 1930, The Mode of Origin and Chromosome Behaviour in Pollen Mother Cells of a Tetraploid Seedling Tomato. *J. Genet.*, **22**, 419–425.

LEVAN, A., 1932, Cytological Studies in *Allium* II., Chromosome morphological contributions. *Hereditas*, **16**, 257–294.

LEWITSKY, G. A., 1931, Experimentally induced alterations of the morphology of chromosomes. *Amer. Nat.*, **65**, 564–567.

LEWITSKY, G. A., and BENETZKAIA, G. K., 1929, Cytological Investigations of constant intermediate rye-wheat hybrids. *Proc. U.S.S.R. Cong. in Genet.*, **2**, 345–352 (English summary).

LEWITSKY, G. A., and KUZMINA, N. E., 1927, Karyological investigations on the genus *Festuca*. *Bull. Appl. Bot.*, **17** (3), 3–36.

LEWITSKY, G. A., and TRON, E. J., 1930, Zur Frage der karyotypische Evolution der Gattung Muscari Mill. *Planta*, **9**, 760–775.

LI, J-C., 1927, The Effect of chromosome aberrations on development in *Drosophila melanogaster*. *Genetics*, **12**, 1–58.

LIDFORSS, B., 1914, Résumé seiner Arbeiten über Rubus. *Z.I.A.V.*, **12**, 1–13.

LINDENBEIN, W., 1927, Beiträge zur Cytologie der Charales. *Planta*, **4**, 437–466.

LINDSTROM, E. W., 1929, A haploid mutant in the tomato. *J. Hered.*, **20**, 23–30.

LINDSTROM, E. W., and KOOS, K., 1931, Cytogenetic investigations of a haploid tomato and its diploid and tetraploid progeny. *Amer. J. Bot.*, **18**, 398–410.

LJUNGDAHL, H., 1922, Zur Zytologie der Gattung *Papaver*. Vorläufige Mitteilung. *Sv. Bot. Tidsskr.*, **16**, 103–114.

LJUNGDAHL, H., 1924, Über die Herkunft der in der Meiosis konjugierenden Chromosomen bei Papaver-Hybriden. *Sv. Bot. Tidsskr.*, **18**, 279–291.

LONGLEY, A. E., 1924, Chromosomes in Maize and Maize Relatives. *J. Agric. Res.*, **28**, 673–681.

LONGLEY, A. E., 1927, Supernumerary Chromosomes in Zea Mays. *J. Agr. Res.*, **35**, 769–784.

LORBEER, G., 1927, Untersuchungen über die Reduktionsteilung und Geschlechtsbestimmung bei Lebermoosen. *Z.I.A.V.*, **44**, 1–109.

LORBEER, G., 1930, Geschlechtsunterschiede im Chromosomensatz und in der Zellgrösse bei Sphareocarpus Donnellii Aust. *Zeits. f. Bot.*, **23**, 932–956.

LOTSY, J. P., 1905, Die X-Generation und die 2X-Generation. Eine Arbeitshypothese. *Biol. Zbl.*, **25**, 97–117.

LOTSY, J. P., 1925, *Evolution considered in the light of hybridization*. Christchurch, N.Z.

LUCAS, F. F., and STARK, M. B., 1931, A Study of Living Sperm Cells of Certain Grasshoppers by means of the Ultraviolet Microscope. *J. Morphol.*, **52**, 91–107.

McClintock, B., 1929 *a*, A cytological and genetical study of triploid maize. *Genetics*, **14**, 180–222.

McClintock, B., 1929 *b*, A method for making Aceto-carmin smears permanent. *Stain Tech.*, **4**, 53–56.

McClintock, B., 1929 *c*, A 2n-1 Chromosomal Chimaera in Maize. *J. Hered.*, **20**, 218.

McClintock, B., 1931 *a*, A Cytological Demonstration of the Location of an Interchange between the non-homologous chromosomes of Zea Mays. *Proc. Nat. Acad. Sci.*, **16**, 791–796.

McClintock, B., 1931 *b*, The order of the genes *C Sh* and *Wx* in *Zea Mays* with reference to a Cytologically Known Point in the Chromosome. *Proc. Nat. Acad. Sci.*, **17**, 485–491.

McClung, C. E., 1905, The chromosome complex of orthopteran spermatocytes. *Biol. Bull.*, **9**, 304–340.

McClung, C. E., 1914, A comparative study of the chromosomes in orthopteran spermatogenesis. *J. Morphol.*, **25**, 651–749.

McClung, C. E., 1917, The multiple chromosomes of Hesperotettix and Mermiria. *J. Morphol.*, **29**, 519–605.

McClung, C. E., 1927 *a*, Synapsis and Related Phenomena in Mecostethus and Leptysma. (Orthoptera.) *J. Morphol. Physiol.*, **43**, 181–264.

McClung, C. E., 1927 *b*, The Chiasmatype Theory of Janssens. *Quart. Rev. Biol.*, **2**, 344–366.

McClung, C. E., 1928 *a*, The Generic Constancy of a Particular Chromosome in Mecostethus Gracilis, Lineatus and Grossus. *Arch. Biol.*, **38**, 503–528.

McClung, C. E., 1928 *b*, Differential Chromosomes of *Mecostethus gracilis*. *Zeits. f. Zellforsch. u. mikr. Anat.*, **7**, 756–778.

Mäckel, H. G., 1928, Zur Cytologie einiger Saprolegniaceen. *Jahrb. wiss. Bot.*, **69**, 517–548.

McNabb, J. W., 1928, A study of the chromosomes in meiosis, fertilization and cleavage in the grasshopper egg (Orthoptera). *J. Morphol.*, **45**, 47–93.

Maeda, T., 1928, The Spiral Structure of Chromosomes in the sweet-pea (*Lathyrus odoratus* L.). *Bot. Mag. Tokyo*, **42**, 191–195.

Maeda, T., 1930 *a*, The Meiotic Divisions in the Pollen Mother Cells of the Sweet-pea (Lathyrus odoratus L.) with special reference to the Cytological Basis of Crossing-over. *Mem. Coll. Sci. Kyoto* B., **5**, 89–123.

Maeda, T., 1930 *b*, On the Configurations of Gemini in the Pollen Mother Cells of *Vicia Faba*, L. *Mem. Coll. Sci. Kyoto* B, **5**, 125–137.

Maeda, T., and Kato, K., The Pollen Mother Cells of *Spinacia oleracea*, Mill. and *Vicia Faba*, L. *Mem. Coll. Sci. Kyoto* B, **4**, 327–345.

Mainx, F., 1924, Versuche über die Beeinflussung der Mitose durch Giftstoffe. *Zool. Jahrb.*, **41**, 553–580.

Mainx, F., 1931, Physiologische und genetische Untersuchungen an Œdogonien I. *Zeits. f. Bot.*, **24**, 481–527.

Malan, D. E., 1918, Ergebnisse anatomischer Untersuchungen an Standfuss'schen Lepidopteren-Bastarden. *Mitt. Entom. Zurich*, **4**, 201–260.

Mangelsdorf, P. C., and Reeves, R. G., 1931, Hybridization of Maize, Tripsacum and Euchlæna. *J. Hered.*, **22**, 329–343.

Manton, I., 1932 *a*, Contributions to the Cytology of Apospory in *Osmunda regalis* L. *J. Genet.*, **25**, 423–430.

Manton, I., 1932 *b*, Introduction to the Cytology of the Cruciferæ. *Ann. Bot.* (In the press.)

Marchal, El., and Marchal, Em., 1911, Aposporie et Sexualité chez les Mousses III. *Bull. Acad. Roy. Belg.*, 9–10, 1911, 750–778.

Marchal, Em., 1912, Recherches cytologiques sur le genre "*Amblystegium.*" *Bull. Soc. Roy. Bot. Belg.*, **51,** 189–203.

Marsden-Jones, E. M., and Turrill, W. B., 1930, The History of a Tetraploid Saxifrage. *J. Genet.*, **23,** 83–92.

Martens, P., 1928, Le cycle du chromosome somatique dans les phanérogames. III. Recherches expérimentales sur la cinèse dans la cellule vivante. *Cellule*, **38,** 69–174.

Mather, K., 1932, Chromosome Variation in *Crocus*, I. *J. Genet.* (In the press.)

Matsuda, H., 1928, On the origin of big pollen grains with an abnormal number of chromosomes. *Cellule*, **38,** 215–243.

Matthey, R., 1929, Les Chromosomes de la Vipère male (Vipera aspis, Lin.). *Biol. Zbl.*, **49,** 35–43.

Matthey, R., 1931, Chromosomes de Reptiles Sauriens, Ophidiens et Cheloniens. L'Évolution de la formule chromosomiale chez les Sauriens. *Rev. suisse Zool.*, **38,** 117–186.

Meijere, see Meyere.

Melburn, M. C., 1929, Heterotypic prophases in the absence of chromosome pairing. *Canad. J. Res.*, **1,** 512–527.

Melburn, M. C., and Thompson, W. P., 1927, The cytology of a tetraploid wheat hybrid (*Triticum spelta* × *T. monococcum*). *Amer. J. Bot.*, **14,** 327–333.

Messeri, A., 1930, Il numero dei cromosomi dell' *Allium roseum* v. *bulbilliferum* e dell' *A.* confr. *odorum* e nuovo esempi di rapporti fra apomissia e poliploidismo. *N. Gior. Bot. Ital.*, **37,** 276–277.

Messeri, A., 1931, Ricerche embriologiche e cariologiche sopra i generi "Allium" e "Nothoscordon." *Nuov. Giorn. Bot. Ital.*, **38,** 409–441.

Metcalf, M. M., 1928, Trends in Evolution: A discussion of data bearing upon "orthogenesis." *J. Morphol.*, **45,** 1–45.

Metz, C. W., 1922, Association of homologous chromosomes in tetraploid cells of Diptera. *Biol. Bull.*, **43,** 369–373.

Metz, C. W., 1926, Observations on Spermatogenesis in Drosophila. *Zeits. f. Zellforsch. u. mikr. Anat.*, **4,** 1–28.

Metz, C. W., Moses, M. S., and Hoppe, E. N., 1926, Chromosome Behavior and Genetic Behavior in Sciara (Diptera). I. *Z.I.A.V.*, **42,** 237–270.

Metz, C. W., and Nonidez, J. F., 1921, Spermatogenesis in the fly, Asilus sericeus. Say. *J. Exp. Zool.*, **32,** 165–185.

Metz, C. W., and Nonidez, J. F., 1923, Spermatogenesis in *Asilus notatus*, Wied. (Diptera). *Arch. f. Zellforsch.*, **17,** 438–449.

Metz, C. W., and Nonidez, J. F., 1924, The behavior of the nucleus and chromosomes during spermatogenesis in the robber fly, *Lasiopogon bivittatus*. *Biol. Bull.*, **46,** 153–164.

Meurman, O., 1925, The Chromosome Behaviour of some Diœcious Plants and their Relatives with Special Reference to the Sex Chromosomes. *Comm. Biol. Soc. Sci. Fenn.*, **2** (3), 1–104.

Meurman, O., 1928, Cytological Studies in the Genus Ribes L. *Hereditas*, **11,** 289–356.

Meurman, O., 1929 *a*, Association and Types of Chromosomes in *Aucuba japonica*. *Hereditas*, **12,** 179–209.

Meurman, O., 1929 *b*, Prunus laurocerasus L., a Species showing High Polyploidy. *J. Genet*, **21,** 85–94.

Meyer, K. J., 1925, Parthenogenesis bei Thismia javanica im Lichte der Haberlandtschen Anschauung. *Ber. Deuts. Bot. Ges.*, **43,** 193–197.

Meyere, J. H. C. de, 1928, Über haltbare rasche Färbung vermittels Azetokarmin. *Zeits. wiss. Mikr.*, **46,** 189–195.

MEYERE, J. H. C. de, *as* MEIJERE, J. C. H. de, 1930, Über einige europäische Insekten, besonders günstig zum Studium der Reifungsteilungen, nebst einigen Zusätzen zur Azetokarminmethode. *Zool. Anzeig.*, **88,** 209–219.

MICHAELIS, P., 1926, Über den Einfluss der Kälte über die Reduktionsteilung von Epilobium. *Planta* **1,** 569–582.

MICHAELIS, P., 1930, Über experimentell erzeugte, heteroploide Pflanzen von Œnothera Hookeri. *Zeits. f. Bot.*, **23,** 288–308.

MICZYNSKI, K., 1931, Genetic studies in the genus Ægilops II. The morphology and cytology of the interspecific hybrids. *Bull. Acad. Pol.* (B), **1,** 51–82.

MINOUCHI, O., 1929 *a,* Chromosome Arrangement, VI. The Behaviour of Chromosomes from the Moment of Disappearance of the Nuclear Membrane up to the Formation of the Equatorial Plate in the First Spermatocyte Division of the Albino Rat. *Mem. Coll. Sci. Kyoto* B, **4,** 323–326.

MINOUCHI, O., 1929 *b,* On the Spermatogenesis of the Racoon Dog (Nyctereutes viverrinus), with special reference to the Sex Chromosomes. *Cytologia,* **1,** 88–108.

MIYAJI, Y., 1929, Studien über die Zahlenverhältnisse der Chromosomen bei der Gattung *Viola. Cytologia,* **1,** 28–58.

MODILEWSKI, J., 1930, Neue Beiträge zur Polyembryonie von *Allium odorum. Ber. Deuts. Bot. Ges.*, **48,** 285–294.

MOFFETT, A. A., 1931 *a,* A preliminary account of chromosome behaviour in the Pomoideæ. *J. Pomol.*, **9,** 100–110.

MOFFETT, A. A., 1931 *b,* The Chromosome Constitution of the Pomoideæ. *Proc. Roy. Soc. B,* **108,** 423–446.

MOFFETT, A. A., 1932 *a,* Studies on the Formation of Multinuclear Giant Pollen Grains in *Kniphofia. J. Genet.*, **25,** 315–337.

MOFFETT, A. A., 1932 *b,* Chromosome Studies in *Anemone,* I. A new type of chiasma behaviour. *Cytologia,* **3.** (In the press.)

MOHR, O. L., 1915, Sind die Heterochromosomen wahre Chromosomen? Untersuchungen über ihr Verhalten in der Ovogenese von *Leptophyes punctatissima. Arch. f. Zellforsch.*, **14,** 151–176.

MOHR, O., 1932, Genetical and cytological proof of somatic elimination of the fourth chromosome in *Drosophila melanogaster. Genetics,* **17,** 60–80. (Cf. *Arch. Biol.*, **42,** 365–373.)

MOL, W. E. de, 1921, De l'éxistence de variétés hétéroploides de l'Hyacinthus orientalis L. dans les cultures hollandaises. *Arch. Néerl. Sci.* III B, **4,** 18–117.

MOL, W. E. de, 1923, Duplication of generative nuclei by means of physiological stimuli and its significance. *Genetica,* **5,** 225–272.

MOL, W. E. de, 1928, Nucleolar number and size in Diploid, Triploid and Aneuploid Hyacinths. *Cellule,* **38,** 1–65.

MOL, W. E. de, 1929, The Originating of Diploid and Tetraploid Pollen Grains in Duc van Thol-Tulips (Tulipa suaveolens) dependent on the method of culture applied. *Genetica,* **11,** 119–212.

MONTGOMERY, T. H., 1901, A Study of the chromosomes of germ cells of Metazoa. *Trans. Amer. Phil. Soc.*, **20,** 154–236.

MONTGOMERY, T. H., 1911, The Spermatogenesis of an hemipteron, *Euchistus. J. Morphol.*, **22,** 731–799.

MORGAN, L. V., 1922, Non-criss-cross inheritance in Drosophila melanogaster. *Biol. Bull.*, **42,** 267–274.

MORGAN, T. H., 1911, Random Segregation versus Coupling in Mendelian Inheritance. *Science* n.s., **34,** 384.

MORGAN, T. H., 1912, The elimination of the sex chromosomes from the male-producing eggs of Phylloxerans. *J. Exper. Zool.*, **12,** 479–498.

Morgan, T. H., 1915, The predetermination of sex in phylloxerans and aphids. *J. Exper. Zool.*, **19**, 285–321.

*Morgan, T. H., 1922, On the Mechanism of Heredity. *Proc. Roy. Soc.* B, **94**, 162–197.

*Morgan, T. H., 1926, *The Theory of the Gene.* New Haven.

Morgan, T. H., 1927, The Constitution of the Germ Material in Relation to Heredity. *Carneg. Inst. Yearbk.*, **26**, 284–288.

Morgan, T. H., and Bridges, C. B., 1919, The origin of gynandromorphs. *Carneg. Inst. Pub.*, **278**, 1–122.

*Morgan, T. H., Bridges, C. B., and Sturtevant, A. H., 1925, The Genetics of Drosophila. *Bibliogr. Genet.*, **2**, 1–262.

Morgan, W. P., 1928, A comparative study of spermatogenesis of five species of earwigs. *J. Morph.*, **46**, 241–273.

Morinaga, T., 1929, Interspecific Hybridization in *Brassica* II. The Cytology of F_1 Hybrids of *B. cernua* and Various other Species with 10 Chromosomes. *Jap. J. Bot.*, **4**, 277–289.

Morinaga, T., and Fukushima, E., 1931, Preliminary Report on the Haploid Plant of Rice, *Oryza sativa* L. *Proc. Imper. Acad.*, Tokyo, **7**, 383–384.

Morinaga, T., Fukushima, E., Kanto, T., Maruyama, Y., and Yamasaki, Y., 1929, Chromosome Numbers of Cultivated Plants II. *Bot. Mag. Tokyo*, **43**, 589–592.

Müller, H. A. C., 1912, Kernstudien an Pflanzen, I und II. *Arch. f. Zellforsch.*, **8**, 1–51.

Muller, H. J., 1916, The Mechanism of Crossing-Over, II. *Amer. Nat.*, **50**, 193–221, 284–305, 350–366, 421–434.

Muller, H. J., 1918, Genetic variability, twin hybrids, and constant hybrids in a case of balanced lethal factors. *Genetics*, **3**, 422–499.

Muller, H. J., 1925 *a*, The regionally differential effect of X-rays on crossing-over in autosomes of *Drosophila*. *Genetics*, **10**, 470–507.

Muller, H. J., 1925 *b*, Why Polyploidy is rarer in Animals than in Plants. *Amer. Nat.*, **59**, 346–353.

Muller, H. J., 1928, The Production of Mutations by X-Rays. *Proc. Nat. Acad. Sci.*, **14**, 714–726.

*Muller, H. J., 1930 *a*, Radiation and Genetics. *Amer. Nat.*, **64**, 220–251

Muller, H. J., 1930 *b*, Types of Visible Variations Induced by X-Rays in *Drosophila*. *J. Genet.*, **22**, 299–334.

Muller, H. J., 1930 *c*, *Œnothera*-like Linkage of Chromosomes in *Drosophila*. *J. Genet.*, **22**, 335–357.

Muller, H. J., 1932, Some Genetic Aspects of Sex. *Amer. Nat.*, **66**, 118–138.

Mulsow, K., 1912, Der Chromosomencyclus bei Ancyracanthus cystidicola Rud. *Arch. f. Zellforsch.*, **9**, 63–72.

Müntzing, A., 1927, Chromosome Number, Nuclear Volume and Pollen Grain Size in *Galeopsis*. *Hereditas*, **10**, 241–260.

Müntzing, A., 1928, Pseudogamie in der Gattung *Potentilla*. *Hereditas*, **11**, 267–283.

Müntzing, A., 1930 *a*, Outlines to a Genetic Monograph of the Genus *Galeopsis*. *Hereditas*, **13**, 185–341.

Müntzing, A., 1930 *b*, Über Chromosomenvermehrung in *Galeopsis*-Kreuzungen und ihre phylogenetische Bedeutung. *Hereditas*, **14**, 153–172.

Müntzing, A., 1931, Note on the Cytology of some Apomictic *Potentilla* Species. *Hereditas*, **15**, 166–178.

Müntzing, A., 1932, Cyto-Genetic Investigations on Synthetic *Galeopsis Tetrahit*. *Hereditas*, **16**, 105–154.

Nachtsheim, H., 1913, Cytologische Studien über die Geschlechtsbestimmung bei der Honigbiene (Apis mellifica L.). *Arch. f. Zellforsch.*, **11,** 169–241.

Nagao, S., 1929, Karyological studies of the Narcissus plant. I. Somatic Chromosome Number of Some Garden Varieties and Some Meiotic Phases of a Triploid Variety. *Mem. Coll. Sci. Kyoto B*, **4,** 175–198.

Nakamura, T., 1929, Chromosome Arrangement IX. The Pollen Mother Cells in *Cycas revoluta* Thunb. *Mem. Coll. Sci. Kyoto* B, **4,** 353–369.

Nakamura, K., 1931, Studies on Reptilian Chromosomes, II. On the chromosomes of *Eumeces latiscutatus* (Hallowell), a Lizard. *Cytologia*, **2,** 385–400.

Navashin, M., 1926, Variabilität des Zellkerns bei Crepis-Arten in Bezug auf die Artbildung. *Zeits. f. Zellforsch. u. mikr. Anat.*, **4,** 171–215.

Navashin, M., as Nawaschin, 1927 *a*, Ein Fall von Merogonie infolge Artkreuzung bei Compositen. *Ber. Deuts. Bot. Ges.*, **45,** 115–126.

Navashin, M., 1927 *b*, Über die Veränderungen von Zahl und Form der Chromosomen infolge der Hybridisation. *Zeits. f. Zellforsch. u. mikr. Anat.*, **6,** 195–233.

Navashin, M., 1930 *a*, Unbalanced Somatic Chromosomal Variation in Crepis. *Univ. Calif. Pub. Agr. Sci.*, **6,** 95–106.

Navashin, M., 1930 *b*, *Zacintha verrucosa* Gärtner : another plant with Six Somatic Chromosomes. *Nature*, **126,** 604.

Navashin, M., 1931 *a*, Spontaneous Chromosome Alterations in Crepis tectorum L. *Univ. Calif. Pub. Agr. Sci.*, **6,** 201–206.

Navashin, M., 1931 *b*, Chromatin Mass and Cell Volume in related species. *Univ. Calif. Pub. Agr. Sci.*, **6,** 207–230.

Navashin, M., 1931 *c*, A Preliminary Report on some Chromosome Alterations by X-Rays in *Crepis*. *Amer. Nat.*, **65,** 243–252.

Naville, A., 1923, Recherches sur la constance numérique des Chromosomes dans la lignée germinale mâle de *Helix pomatia* L. *Rev. suisse Zool.*, **30,** 353–385.

Naville, A., 1931, Les Sporozoaires (cycles chromosomiques et sexualité). *Mem. Soc. Phys. Hist. Nat. Genève*, **41,** 1–223.

Nawaschin, S., 1912, Über den Dimorphismus der Zellkerne in den somatischen Zellen von *Galtonia candicans*. *Bull. Acad. Imp. Sci. Petersb. VI.*, **6,** 373–385. (*See also :* Babcock.)

Nebel, B., 1929, Zur Cytologie von Malus und Vitis. *Gartenbauwiss.*, **1,** 549–592.

Nemec, B., 1910, *Das Problem des Befruchtungsvorgänge.* Berlin.

Nemec, B., 1926, Multipolare Teilungsfiguren und vegetative Chromosomenreduktion. *Biol. Gen.*, **2,** 96–103.

Nemec, B., 1929 *a*, Über Struktur und Aggregatzustand des Zellkerns. *Protoplasma*, **7,** 423–443.

Nemec, B., 1929 *b*, Multipolare Teilungen in chloralisierten Wurzeln. *Mem. Soc. Roy. Sci. Bohème* (Prague), **2** (4), 1–7.

Newton, W. C. F., 1927, Chromosome Studies in *Tulipa* and Some Related Genera. *J. Linn. Soc.* (Bot.), **47,** 339–354.

Newton, W. C. F., and Darlington, C. D., 1929, Meiosis in Polyploids I. *J. Genet*, **21,** 1–16.

Newton, W. C. F., and Darlington, C. D., 1930, *Fritillaria Meleagris :* Chiasma-Formation and Distribution. *J. Genet*, **22,** 1–14.

Newton, W. C. F., and Pellew, C., 1929, *Primula kewensis* and its derivatives. *J. Genet.*, **20,** 405–467.

Nishiyama, I., 1928, Reduction Division in *Lycoris*. *Bot. Mag. Tokyo*, **42,** 509–513.

Nishiyama, I., 1929, The Genetics and Cytology of Certain Cereals. I. Morphological and Cytological Studies on Triploid, Pentaploid and Hexaploid *Avena* Hybrids. *Jap. J. Genet.*, **5,** 1–48.

NISHIYAMA, I., 1931, The Genetics and Cytology of Certain Cereals II. Karyo-Genetic Studies of Fatuoid Oats with special reference to their origin. *Jap. J. Genet.*, **7,** 49–102.

OGUMA, K., 1921, The idiochromosomes of the mantis. *J. Coll. Agr. Imp. Univ. Hokkaido*, **10,** 1–27.
OHMACHI, F., 1929 *a*, A Short Note on the Chromosomes of *Gryllus campestris*, L., in Comparison with those of *Gryllus mitratus*, Burm. *Proc. Imp. Acad. Tokyo*, **5,** 357–359.
OHMACHI, F., 1929 *b*, A Short Note on the Chromosomes of *Gryllotalpa africana* Pal. *Proc. Imp. Acad. Tokyo*, **5,** 360–363.
OHMACHI, F., 1929 *c*, Preliminary Note on a Case of Facultative Parthenogenesis in Loxoblemmus frontalis, Shir. (Gryllidæ). *Proc. Imp. Acad. Tokyo*, **5,** 367–369.
OKABE, S., 1928, Zur Zytologie der Gattung *Prunus*. *Sc. Rep. Tohoku Imp. Univ.*, Ser. 4, **3,** 733–743.
OKABE, S., 1929 *a*, Über eine tetraploide Gartenrasse von *Psilotum nudum*, Palisot de Beauvois (= *P. triquetum* Sw.) und die tripolige Kernteilung in ihren Sporenmutterzellen. *Sc. Rep. Tohoku Imp. Univ.*, Ser. 4, **4,** 373–380.
OKABE, S., 1929 *b*, Meiosis im Oogonium von *Sargassum Horneri* (Turn.) Ag. *Sc. Rep. Tohoku Imp. Univ.*, Ser. 4, **4,** 661–669.
O'MARA, J., 1931, Chromosome Pairing in *Yucca flaccida*. *Cytologia*, **3,** 66–76.
ONO, T., 1927, Reducing Division in Triploid *Primula*. A preliminary note. *Bot. Mag. Tokyo*, **41,** 601–604. (English summary.)
ONO, T., 1928, Further investigations on the cytology of *Rumex*. *Bot. Mag. Tokyo*, **42,** 524–533. (English summary.)
ONO, T., 1930 *a*, Further investigations on the cytology of *Rumex*. V–VII. *Bot. Mag. Tokyo*, **44,** 168–176. (English summary.)
ONO, T., 1930 *b*, Chromosomenmorphologie von *Rumex Acetosa*. *Sc. Rep. Tohoku Imp. Univ.*, Ser. 4, **5,** 415–422.
ONO, T., and SHIMOTOMAI, N., 1928, Triploid and Tetraploid intersex of *Rumex Acetosa*, L. *Bot. Mag. Tokyo*, **42,** 266–270.
OSAWA, J., 1913, Studies on the cytology of some species of Taraxacum. *Arch. f. Zellforsch.*, **10,** 450–469.
OSAWA, J., 1920, Cytological and Experimental Studies in Morus with special reference to triploid mutants. *Bull. Imp. Ser. Sta. Tokyo*, **1,** 317–369.
OSTENFELD, C. H., 1910, Further studies on the Apogamy and Hybridisation of the Hieracia. *Z.I.A.V.*, **3,** 241–285.
OSTENFELD, C. H., 1921, Some Experiments on the Origin of New Forms in the genus *Hieracium* sub-genus *Archieracium*. *J. Genet.*, **11,** 117–122.
OSTENFELD, C. H., and ROSENBERG, O., 1907, Experimental and Cytological Studies in the Hieracia II. O. Rosenberg: Cytological studies on the apogamy in *Hieracium*. *D. Bot. Tidsskr.*, **28,** 143–170.
OVEREEM, C. VAN, 1921, Über Formen mit abweichender Chromosomenzahl bei Œnothera. *Beih. Bot. Zbl.*, **38,** 73–113.
OVEREEM, C. VAN, 1922, Über Formen mit abweichender Chromosomenzahl bei *Œnothera*. Fortschritt. *Beih. Bot. Zbl.*, **39,** 1–80.
OVERTON, J. B., 1909, On the Organisation of the Nuclei in the Pollen-Mother-Cells of certain plants, with special reference to the Permanence of the Chromosomes. *Ann. Bot.*, **23,** 19–61.

PACE, L., 1913, Apogamy in Atamasco. *Bot. Gaz.*, **56,** 376–394.
PAINTER, T. S., 1921, Studies in reptilian spermatogenesis I. The spermatogenesis of lizards. *J. Exper. Zool.*, **34,** 281–327.

Painter, T. S., 1924, Studies in mammalian spermatogenesis III. The fate of the chromatin-nucleolus in the opossum. *J. Exper. Zool.*, **39**, 197–247.

Painter, T. S., 1925, A Comparative Study of the Chromosomes of Mammals. *Amer. Nat.*, **59**, 385–409.

Painter, T. S., 1927, The Chromosome Constitution of Gates' "Non-disjunction" (v-o) Mice. *Genetics*, **12**, 379–392.

Painter, T. S., and Muller, H. J., 1929, Parallel Cytology and Genetics of induced translocations and deletions in Drosophila. *J. Hered.*, **20**, 287–298.

Pariser, K., 1927, Die Zytologie und Morphologie der triploiden Intersexe des rückgekreuzten Bastards von *Saturnia pavonia* L. und *Saturnia pyri* Schiff. *Zeits. f. Zellforsch. u. mikr. Anat.*, **5**, 415–447.

Patterson, J. T., and Muller, H. J., 1930 *d*, Are "Progressive" Mutations produced by X-rays? *Genetics*, **15**, 495–578.

Payne, F., 1914, Chromosomal variations and the formation of the spermatocyte chromosomes in the European earwig, *Forficula* sp. *J. Morphol.*, **25**, 559–585.

*Peacock, A. D., 1925, Animal Parthenogenesis in relation to Chromosomes and Species. *Amer. Nat.*, **59**, 218–224.

Pearson, N. E., 1927, A Study of Gynandromorphic Katydids. *Amer. Nat.*, **61**, 283–285.

Pellew, C., and Sansome, E. Richardson, 1931, Genetical and Cytological Studies on the Relations between European and Asiatic Varieties of *Pisum sativum*. *J. Genet.*, **25**, 25–54.

Percival, J., 1930, Cytological Studies of some Hybrids of *Ægilops* sp. x Wheats, and of some Hybrids between different Species of *Ægilops*. *J. Genet.*, **22**, 201–278.

Peto, F. H., 1930, Cytological Studies in the Genus *Agropyron*. *Canad. J. Res.*, **3**, 428–448.

Peto, F. H., 1932, The Cytology of certain Intergeneric Hybrids between *Festuca* and *Lolium*. *J. Genet.* (In the press.)

Philp, J., and Huskins, C. L., 1931. The Cytology of *Matthiola incana* R. Br., especially in relation to the Inheritance of Double Flowers. *J. Genet.*, **24**, 359–404.

Pietschmann, Käthe, 1929, Untersuchungen an Vahlkampfia tachypoda Gläser. *Arch. Prot.*, **65**, 379–425.

Plough, H. H., 1917, The Effect of Temperature on Crossing-over in *Drosophila*. *J. Exper. Zool.*, **24**, 147–209.

Poole, C. F., 1931, The Interspecific Hybrid Crepis rubra × C. fœtida and Some of its Derivatives, I. *Univ. Calif. Pub. Agr. Sci.*, **6**, 169–200.

Poole, C. F., 1932, The interspecific hybrid, Crepis rubra × C. fœtida, and some of its derivatives. II. Two selfed generations from an amphidiploid hybrid. *Univ. Calif. Pub. Agr. Sci.*, **6**, 231–255.

*Punnett, R. C., 1925, *Lathyrus odoratus*. *Bibliograph. Genet.*, **1**, 69–82.

Randolph, L. F., 1928, Chromosome Numbers in Zea Mays L. *Cornell Univ. Exp. Sta.* (Ithaca) *Mem.*, 117.

Randolph, L. F., and McClintock, B., 1926, Polyploidy in Zea Mays L. *Amer. Nat.*, **60**, 99–102.

Redfield, H., 1930, Crossing-over in the third chromosomes of triploids o *Drosophila melanogaster*. *Genetics*, **15**, 205–252.

Renner, O., 1919 *a*, Zur Biologie und Morphologie der männlichen Haplonten einiger Önotheren. *Zeits. f. Bot.*, **11**, 305–380.

Renner, O., 1919 *b*, Über Sichtbarwerden der Mendelschen Spaltung im Pollen von Önotherabastarden. *Ber. Deuts. Bot. Ges.*, **37**, 129–135.

Renner, O., 1921, Heterogamie im weiblichen Geschlecht und Embryosackentwicklung bei den Önotheren. *Zeits. f. Bot.*, **13**, 609–621.

Renner, O., 1925, Untersuchungen über die faktorielle Konstitution einiger komplexheterozygotischer Önotheren. *Biblioth. Genet.*, **9**, 1–168.

Renner, O., 1927, Über eine aus *Œnothera suaveolens* durch Bastardierung gewonnene homozygotische *lutescens*-Form. *Hereditas*, **9**, 69–80.

*Renner, O., 1929, Artbastarde bei Pflanzen. *Handb. d. Vererbungswissenschaft*, **2.** (*See also :* Hœppener.)

*Reuter, E., 1930, Beiträge zu einer einheitlichen Auffassung gewisser Chromosomenfragen. *Act. Zool. Fenn.*, **9**, 1–487.

Rhoades, M. M., 1931, The frequencies of homozygosis of factors in attached-X females of *Drosophila melanogaster*. *Genetics*, **16**, 375–385.

Robertson, W. R. B., 1915, Chromosome Studies III. Inequalities and deficiencies in homologous chromosomes : their bearing upon synapsis and the loss of unit characters. *J. Morphol.*, **26**, 109–141.

Robertson, W. R. B., 1916, Chromosome Studies I. Taxonomic relationships shown in chromosomes of Tettigidæ and other subfamilies of the Acrididæ : V-shaped chromosomes and their significance in Acrididæ, Locustidæ, and Gryllidæ : chromosomes and variation. *J. Morphol.*, **27**, 179–332.

Robertson, W. R. B., 1930, Chromosome Studies V. Diploidy and persistent chromosome relations in partheno-produced Tettigidæ (Apotettix eurycephalus and Paratettix texanus). *J. Morphol.*, **50**, 209–257.

Robertson, W. R. B., 1931 *a*, Hybrid Vigor—a Factor in Tettigid Parthenogenesis ? *Amer. Nat.*, **65**, 165–172.

Robertson, W. R. B., 1931 *b*, A split in chromosomes about to enter the spermatid (Paratettix texanus). *Genetics*, **16**, 349–352.

Robertson, W. R. B., 1931 *c*, On the origin of partheno-produced males in Tettigidæ Apotettix and Paratettix. *Genetics*, **16**, 353–356.

Robertson, W. R. B., 1931 *d*, Chromosome Studies II. Synapsis in the Tettigidæ, with special reference to the presynapsis split. *J. Morphol.*, **51**, 119–139.

Rohweder, H., 1929, Über Kernuntersuchungen an *Dianthus*-Arten (Vorl. Mitt.). *Ber. Deuts. Bot. Ges.*, **47**, 81–86.

Rosenberg, O., 1906, Über die Embryobildung in der Gattung Hieracium. *Ber. Deuts. Bot. Ges.*, **24**, 157–161.

Rosenberg, O., 1909, Cytologische und morphologische Studien an Drosera longifolia × rotundifolia. *K. Sv. Vet. Handl.*, **43** (11), 1–64.

Rosenberg, O., 1912, Über die Apogamie bei *Chondrilla juncea. Svensk Bot. Tidsskr.*, **6**, 915–919.

Rosenberg, O., 1917, Die Reduktionsteilung und ihre Degeneration in Hieracium. *Svensk Bot. Tidsskr.*, **11**, 145–206.

Rosenberg, O., 1927, Die Semiheterotypische Teilung und ihre Bedeutung für die Entstehung verdoppelter Chromosomenzahlen. *Hereditas*, **8**, 305–338.

*Rosenberg, O., 1930, Apogamie und Parthenogenesis bei Pflanzen. *Handb. d. Vererbungswissenschaft*, **2.** (*See also :* Ostenfeld.)

Rückert, J., 1892, Zur Entwicklungsgeschichte des Ovarialeies bei Selachiern. *Anat. Anz.*, **7**, 107–158.

Rudloff, F., 1930, Oe. pachycarpa Renner. Genetische und cytologische Untersuchungen. *Gartenbauwissenschaft*, **3**, 499–526.

Rudloff, F., 1931, Zur Polarisation in der Reduktionsteilung heterogamer Œnotheren I. Die Embryosack-Entwicklung und ihrer Tendenzen. *Z.I.A.V.*, **58**, 422–433.

RUTTLE, M. L., 1927, Chromosome numbers and morphology in *Nicotiana* I. The somatic chromosomes and non-disjunction in *N. alata* var. *grandiflora*. *Univ. Calif. Pub. Bot.*, **11**, 159–176.

RUTTLE, M. L., 1928, Chromosome numbers and morphology in *Nicotiana* II. Diploidy and Partial Diploidy in root-tips of *Tabacum* haploids. *Univ. Calif. Pub. Bot.*, 11, 213–232.

RYBIN, V. A., 1927 *a*, On the number of chromosomes observed in the somatic and reduction divisions of the cultivated apple in connection with pollen sterility of some of its varieties. *Bull. Appl. Bot.*, **17** (3), 101–120.

RYBIN, V. A., 1927 *b*, Polyploid Hybrids of Nicotiana Tabacum L. × Nicotiana rustica L. *Bull. Appl. Bot.*, **17** (3), 191–240.

RYBIN, V. A., 1929, Über einen allotetraploiden Bastard von *Nicotiana tabacum* × *Nicotiana sylvestris*. *Ber. Deuts. Bot. Ges.*, **37**, 385–394.

SAEZ, F. A., 1930, Investigaciones sobre los cromosomas de algunos Ortópteros de la America del Sur. *Rev. Mus. La Plata*, **32**, 317–361.

SAKAMURA, T., 1915, Über die Einschnürung der Chromosomen bei *Vicia Faba* L. *Bot. Mag. Tokyo*, **29**, 287–300.

SAKAMURA, T., 1927 *a*, Chromosomenforschungen an frischem Material. *Protoplasma*, **1**, 537–565.

SAKAMURA, T., 1927 *b*, Fixierung von Chromosomen mit siedendem Wasser. *Bot. Mag. Tokyo*, **41**, 59–64.

SAKAMURA, T., and STOW, I., 1926, Über die experimentell veranlasste Entstehung von keimfähigan Pollenkörner mit abweichenden Chromosomenzahlen. *Jap. J. Bot.*, **3**, 111–137.

SANDS, H. C., 1923, The structure of the chromosomes in *Tradescantia virginica* L. *Amer. J. Bot.*, **10**, 343–360.

SANSOME, E. R., 1932, Segmental Interchange in *Pisum*. *Cytologia*, **3**, 200–219.

SANSOME, F. W., 1931 *a*, Saxifrage Crosses. *Nature*, **127**, 59–60.

SANSOME, F. W., 1931 *b*, Graft Hybrids and Induction of Polyploids in Solanum. *Proc. 9th Int. Hort. Cong.*, 92–99.

SANSOME, F. W., and PHILP, J., 1932, *Recent Advances in Plant Genetics*. London, Churchill.

SANTOS, J. K., 1923, Differentiation among chromosomes in *Elodea*. *Bot. Gaz.*, **75**, 42–59.

SANTOS, J. K., 1924, Determination of sex in Elodea. *Bot. Gaz.*, **77**, 353–376.

SAPĔHIN, A. A., 1928, Hylogenetic Investigations of the Vulgare group in Triticum. *Bull. Appl. Bot.*, **19** (1), 127–166.

SAPĔHIN, L. A., 1931, Über die faktorielle Natur der Unterschiede im Verlaufe der Reduktionsteilung. *Ber. Deuts. Bot. Ges.*, **48**, 443–457.

SASS, J. E., 1929, The cytological basis for homothallism and heterothallism in the Agaricaceæ. *Amer. J. Bot.*, **16**, 663–701.

SAX, K., 1922, Sterility in Wheat Hybrids II. Chromosome behavior in partially sterile hybrids. *Genetics*, **7**, 513–552.

SAX, K., 1929, Chromosome Behavior in Sorbopyrus and Sorbaronia. *Proc. Nat. Acad. Sci.*, **15**, 844–845.

SAX, K., 1930, Chromosome Structure and the Mechanism of Crossing Over. *J. Arnold Arboretum*, **11**, 193–220.

SAX, K., 1931 *a*, The Mechanism of Crossing Over. *Science*, **74**, 41–42.

SAX, K., 1931 *b*, Crossing-Over and Mutation. *Proc. Nat. Acad. Sci.*, **17**, 601–603.

SAX, K., and SAX, H. J., 1924, Chromosome behavior in a genus cross. *Genetics*, **9**, 454–464.

SCHAEDE, R., 1925, Untersuchungen über Zelle, Kern und ihre Teilung am lebenden Objekt. *Beitr. Biol. Pfl.*, **14**, 231–260.

SCHAEDE, R., 1927, Vergleichende Untersuchungen über Cytoplasma, Kern und Kernteilung im lebenden und im fixierten Zustand. *Protoplasma*, **3**, 145–190.

SCHAEDE, R., 1929 *a*, Kritische Untersuchungen über die Mechanik der Karyokinesis. *Planta*, **8**, 383–397.

SCHAEDE, R., 1929 *b*, Die Kolloidchemie des pflanzlichen Zellkernes in der Ruhe und in der Teilung. *Erg. d. Biol.*, **5**, 1–28.

SCHAEDE, R., 1930, Über die Struktur des ruhenden Kernes. *Ber. Deuts. Bot. Ges.*, **48**, 342–348.

SCHIEMANN, E., 1929, Zytologische Beiträge zur Gattung Aegilops. Chromosomenzahlen und Morphologie. (III Mittlg.) *Ber. Deuts. Bot. Ges.*, **47**, 164–181.

SCHRADER, F., 1923 *a*, Haploidie bei einer Spinnmilbe. *Arch. mikr. Anat.*, **97**, 610–622.

SCHRADER, F., 1923 *b*, A study of the chromosomes in three species of *Pseudococcus*. *Arch. Zellforsch.*, **17**, 45–62.

SCHRADER, F., 1925, The cytology of pseudo-sexual eggs in a Species of *Daphnia*. *Z.I.A.V.*, **40**, 1–27.

*SCHRADER, F., 1928, *The Sex Chromosomes*. Berlin.

SCHRADER, F., 1929, Experimental and cytological investigations of the life-cycle of *Gossiparia spuria* (Coccidæ) and their Bearing on the Problem of Haploidy in Males. *Zeits. wiss. Zool.*, **134**, 149–179.

*SCHRADER, F., and HUGHES-SCHRADER, S., 1931, Haploidy in Metazoa. *Quart. Rev. Biol.*, **6**, 411–438.

SCHRADER, F., and STURTEVANT, A. H., 1923, A Note on the theory of sex determination. *Amer. Nat.*, **57**, 379–381.

SCHREINER, A., and SCHREINER, K. E., 1906 *a*, Neue Studien über die Chromatinreifung der Geschlechtszellen. I. Die Reifung der männlichen Geschlechtszellen von Tomopteris onisciformis, Eschscholz. *Arch. Biol.*, **22**, 1–69.

SCHREINER, A., and SCHREINER, K. E., 1906 *b*, Neue Studien über die Chromatinreifung der Geschlechtszellen. II. Die Reifung der männlichen Geschlechtszellen von Salamandra maculosa (Laur.) Spinax niger (Bonap.) und Myxine glutinosa (L.). *Arch. Biol.*, **22**, 419–492.

SCHULTZ, E. S., 1927, Nuclear division and spore-formation in the ascus of *Peziza domiciliana*. *Amer. J. Bot.*, **14**, 307–322.

SCHUSSNIG, B., 1930, Der Chromosomencyclus von *Cladophora Suhriana*. *Œsterr. Bot. Zeits.*, **79**, 273–278.

SCHUSSNIG, B., 1931, Die somatische und heterotype Kernteilung bei Cladophora Suhriana Kützing. *Planta*, **13**, 474–528.

SCHWEMMLE, J., 1926, Vergleichend zytologische Untersuchungen an Onagraceen. II. Die Reduktionsteilung von Eucharidium concinnum. *Jahrb. wiss. Bot.*, **65**, 778–818.

SCHWEMMLE, J., 1928, Genetische und zytologische Untersuchungen an Eu-Œnotheren. *Jahrb. wiss. Bot.*, **67**, 849–876.

SEILER, J., 1914, Das Verhalten der Geschlechtschromosomen bei Lepidopteren. Nebst einem Beitrag zur Kenntnis der Eireifung, Samenreifung und Befruchtung. *Arch. Zellforsch.*, **13**, 159–269.

SEILER, J., 1923, Geschlechtschromosomen-Untersuchungen an Psychiden. IV. Die Parthenogenese der Psychiden. *Z.I.A.V.*, **31**, 1–99

SEILER, J., 1925, Ergebnisse aus Kreuzungen von Schmetterlingsrassen mit verschiedener Chromosomenzahl. *Arch. Jul. Klaus-Stift.*, **1**, 63–117.

Seiler, J., 1927, Ergebnisse aus der Kreuzung parthenogenetischer und zweigeschlechtliche Schmetterlinge. *Biol. Zbl.*, **47**, 426–446.

Seiler, J., and Haniel, C. B., 1921, Das verschiedene Verhalten der Chromosomen im Eireifung und Samenreifung von Lymantria monacha L. *Z.I.A.V.*, **27**, 81–103.

Selim, L. A. G., 1930, A Cytological Study of *Oryza sativa* L. *Cytologia*, **2**, 1–26.

Senjaninova, M., 1927, Beitrag zur vergleichend-karyologische Untersuchung des Linneons Valeriana officinalis L. (sensu-lato). *Zeits. Zellforsch. u. mikr. Anat.*, **5**, 675–679.

Serebrovsky, A. S., 1929, A General Scheme for the Origin of Mutations. *Amer. Nat.*, **63**, 374–378.

Sharp, L. W., 1920, Spermatogenesis in *Blasia*. *Bot. Gaz.*, **69**, 258–268.

*Sharp, L. W., 1925. The factorial interpretation of sex determination. *Cellule*, **35**, 195–235.

Sharp, L. W., 1929, Structure of Large Somatic Chromosomes. *Bot. Gaz.*, **88**, 349–382.

Sheffield, F. M. L., 1929, Chromosome Linkage in Œnothera, with special reference to some F_1 hybrids. *Proc. Roy. Soc.* B., **105**, 207–228.

Shimotomai, N., 1927, Über Störungen der meiotischen Teilungen durch niedrige Temperatur. *Bot. Mag. Tokyo*, **41**, 149–160.

Shimotomai, N., 1928, Karyokinese im Oogonium von *Cystophyllum sisymbrioides*, J. Ag. *Sci. Rec. Tohoku Imp. Univ.* (4), **3**, 577–579.

Shimotomai, N., 1930, Chromosomenzahlen und Phylogenie bei der Gattung Potentilla. *J. Sci. Hiroshima* B2, **1**, 1–11.

Shimotomai, N., 1931 *a*, Bastardierungsversuche bei *Chrysanthemum*, I. *J. Sci. Hiroshima* B2, **1**, 37–54.

Shimotomai, N., 1931 *b*, Über die abnorme Reduktionsteilung in Pollenmutterzellen die einen riesigen oder überzähligen Zwergkerne enthalten. *Bot. Mag. Tokyo*, **45**, 356–363.

Shimotomai, N. and Koyama, Y., 1932, Geschlechtschromosomen bei *Pogonatum inflexum* Lindb. und Chromosomenzahlen bei einigen anderen Laubmoosen. *J. Sci. Hiroshima Univ.* B (2), **1**, 95–101.

Shinke, N., 1929, Chromosome arrangement IV. The Meiotic Divisions in Pollen Mother Cells of *Sagittaria Agniashi*, Makino and *Lythrum salicaria*, L. var. *vulgare*, DC. subvar. *genuina*, Koehne. *Mem. Coll. Sci. Kyoto* B, **4**, 283–308.

Shinke, N., 1930, On the Spiral Structure of Chromosomes in some Higher Plants. *Mem. Coll. Sci. Kyoto* B, **5**, 239–245.

Sinéty, R. de., 1901, Recherches sur la Biologie et l'Anatomie des Phasmes. *Cellule*, **19**, 119–278.

Sinotô, Y., 1929, Chromosome Studies in Some Dioecious Plants, with special reference to the Allosomes. *Cytologia*, **1**, 109–191.

Skovsted, A., 1929, Cytological Investigations of the Genus *Æsculus* L. With some observations on *Æsculus carnea* Willd., a Tetraploid Species Arisen by Hybridisation. *Hereditas*, **12**, 64–70.

Smith, B. G., 1929, The history of the chromosomal vesicles in the segmenting egg of Cryptobranchus allegheniensis. *J. Morphol.*, **47**, 89–133.

Smith, S. G., 1931, Cytology of *Anchusa* and its Relation to the Taxonomy of the Genus. *Nature*, **128**, 493–494.

Sorokin, H., 1927 *a*, Cytological and morphological investigations on gynodimorphic and normal forms of *Ranunculus acris* L. *Genetics*, **12**, 59–83.

Sorokin, H., 1927 *b*, A study of meiosis in *Ranunculus acris*. *Amer. J. Bot.*, **14**, 76–84.

Sorokin, H., 1929, Idiograms, Nucleoli, and Satellites of certain Ranunculaceæ. *Amer. J. Bot.*, **16**, 407–420.

Sprumont, G., 1928, Chromosomes et satellites dans quelques éspèces *d'Ornithogalum*. *Cellule*, **38,** 269–292.

Stadler, L. J., 1929, Chromosome Number and the Mutation Rate in Avena and Triticum. *Proc. Nat. Acad. Sci.*, **15,** 876–881.

Stadler, L. J., 1930, Recovery following Genetic Deficiency in Maize. *Proc. Nat. Acad. Sci.*, **16,** 714–720.

*Stadler, L. J., 1931, The Experimental Modification of Heredity in Crop Plants. I. Induced Chromosomal Irregularities. *Sci. Agric.*, **11,** 557–572.

Stählin, A., 1929, Morphologische und zytologische Untersuchungen an Gramineen. *Wiss. Arch. Landw.* A (Pflanzenbau), **1,** 330–398.

Steere, W. C., 1931, A New and Rapid Method for making permanent aceto-carmin Smears. *Stain Technol.*, **6,** 107–111.

Stenar, H., 1928, Zur Embryologie der *Veratrum*- und *Anthericum*-Gruppen. *Bot. Notiser*, 1928, 357–378.

Stern, C., 1927, Über Chromosomenelimination bei der Taufliege. *Naturwiss.*, **36,** 740–746.

*Stern, C., 1928, Fortschritte der Chromosomentheorie der Vererbung. *Ergeb. d. Biol.*, **4,** 205–359.

Stern, C., 1929 *a*, Über Reduktionstypen der Heterochromosomen von *Drosophila melanogaster*. *Biol. Zbl.*, **49,** 718–735.

Stern, C., 1929 *b*, Untersuchungen über Aberrationen des Y-Chromosoms von *Drosophila melanogaster*. *Z.I.A.V.*, **51,** 253–353.

Stern, C., 1931, Zytologisch-genetische Untersuchungen als Beweise für die Morgansche Theorie des Faktorenaustauschs. *Biol. Zbl.*, **51,** 547–587.

Stern, C., and Ogura, S., 1931, Neue Untersuchungen über Aberrationen des Y-chromosoms von *Drosophila melanogaster*. *Z.I.A.V.*, **58,** 81–121.

Stern, C., and Sekiguti, K., 1931, Analyse eines Mosaikindividuums bei *Drosophila melanogaster*. *Biol. Zbl.*, **51,** 194–199.

Stevens, N. M., 1909 *a*, Further Studies on the Chromosomes of the Coleoptera. *J. Exp. Zool.*, **6,** 101–113.

Stomps, T. J., 1911, Kernteilung und Synapsis bei *Spinacia oleracea* L. *Biol. Zbl.*, **31,** 257–309.

Stomps, T. J., 1930 *a*, Über Parthenogenesis infolge Fremdbefruchtung bei *Œnothera*. *Z.I.A.V.*, **54,** 243–245.

Stomps, T. J., 1930 *b*, Über parthenogenetische Œnothera. *Ber. Deuts. Bot. Ges.*, **48,** 119–126.

Stomps, T. J., 1931, Weiteres über Parthenogenesis bei Œnothera. *Ber. Deuts. Bot. Ges.*, **49,** 258–266.

Stow, I., 1927, A Cytological Study on Pollen Sterility in *Solanum tuberosum* L. *Jap. J. Bot.*, **3,** 217–238.

Stow, I., 1930, Experimental Studies on the Formation of the Embryosac-like Giant Pollen-Grains in the Anther of *Hyacinthus orientalis*. *Cytologia*, **1,** 417–439.

Strasburger, E., 1907, Apogamie bei Marsilia. *Flora*, **97,** 123–191.

Strasburger, 1910, Sexuelle und apogame Fortpflanzung bei Urticaceen. *Jahrb. Wiss. Bot.*, **47,** 245–288.

Sturtevant, A. H., 1925, The effects of unequal crossing-over at the bar locus in *Drospohila*. *Genetics*, **10,** 117–147.

*Sturtevant, A. H., 1926 *a*, Renner's Studies on the Genetics of *Œnothera*. *Quart. Rev. Biol.*, **1,** 283–288.

Sturtevant, A. H., 1926 *b*, A cross-over reducer in Drosophila melanogaster due to inversion of a section of the third chromosome. *Biol. Zbl.*, **46,** 697–702.

STURTEVANT, A. H., 1929, The Genetics of *Drosophila simulans*. *Carnegie Inst. Wash. Pubn.*, **399,** 1–62.

STURTEVANT, A. H., 1931, Known and Probable Inverted Sections of the Autosomes of *Drosophila melanogaster*. *Carneg. Inst. Wash. Pub.*, **421,** 1–27.

STURTEVANT, A. H., and DOBZHANSKY, T., 1930, Reciprocal translocations in Drosophila and their bearing on Œnothera cytology and genetics. *Proc. Nat. Acad. Sci.*, **16,** 533–536.

STURTEVANT, A. H., and PLUNKETT, C. R., 1926, Sequence of corresponding third chromosome genes in *Drosophila melanogaster* and *D. simulans*. *Biol. Bull.*, **50,** 56–60. (*See also :* Morgan.)

SUESSENGUTH, K., 1923, Über die Pseudogamie bei *Zygopetalum Mackayi* Hook. *Ber. Deuts. Bot. Ges.*, **41,** 16–23.

SUGIURA, T., 1925, Meiosis in *Tropæolum majus*, L. *Bot. Mag. Tokyo*, **39,** 47–54.

SUGIURA, T., 1927, Some observations on the meiosis of the pollen mother cells of *Carica papaya*, *Myrica rubra*, *Aucuba japonica*, and *Beta vulgaris*. *Bot. Mag. Tokyo*, **41,** 219–224.

SUGIURA, T., 1928, Cytological Studies on *Tropæolum* II. *Tropæolum peregrinum*. *Bot. Mag. Tokyo*, **42,** 553–556.

SUTTON, W. S., 1902, On the morphology of the chromosome group in Brachystola magna. *Biol. Bull.*, **4,** 24–39.

SWESCHNIKOWA, I., 1928, Die Genese des Kerns im Genus *Vicia*. *Verh. V. Int. Kong. Vererb.*, **2,** 1415–1421.

SWESCHNIKOWA, I., 1929 *a*, *Vicia sativa L.* and *Vicia Cracca L.* *Ann. Timir. Ag. Acad.* (Moscow), **4,** 1–22.

SWESCHNIKOWA, I., 1929 *b*, Reduction Division in the Hybrids of *Vicia* (in *Russian*). *Proc. U.S.S.R. Cong. Genet.*, **2,** 447–452.

SWEZY, O., 1929, Maturation of the Male Germ Cells in the Rat. *J. Morphol.*, **48,** 433–443.

TÄCKHOLM, G., 1922, Zytologische Studien über die Gattung *Rosa*. *Acta Hort. Berg.*, **7,** 97–381.

TAHARA, M., and SHIMOTOMAI, N., 1927, Bastardierung als eine Ursache für die Entstehung der Chromosomenpolyploidie. I. Bastard zwischen *Chrysanthemum marginatun* und *C. lavandulaefolium*. *Sci. Rep. Tohoku Imp. Univ.*, Ser. 4, **2,** 293–299.

TAKAGI, F., 1928, The Influence of Higher Temperature on the Reduction Division of the Pollen Mother-Cells of *Lychnis Sieboldii*, van Houtte. *Sci. Rep. Tohoku Imp. Univ.*, Ser. 4, **3,** 461–466.

TAKAMINE, N., 1927, Some observations on the chromosomes of *Najas major* All. *Bot. Mag. Tokyo*, **41,** 118–122.

TAKENAKA, Y., 1929, Karyological Studies in *Hemerocallis*. *Cytologia*, **1,** 76–83.

TAKENAKA, Y., 1930 *a*, On the Sex-Chromosomes of *Rumex montanus* Desf. *Bot. Mag. Tokyo*, **44,** 176–185.

TAKENAKA, Y., 1930 *b*, On the Chromosomes of *Lycoris squamigera* Maxim. *J. Nat. Hist. Soc. Korea*, **10,** 54–56. Abstr. *Jap. J. Bot.*, **5** (80).

TAKENAKA, Y., and NAGAMATSU, S., 1930, On the Chromosomes of *Lilium tigrinum* Ker. *Bot. Mag. Tokyo*, **44,** 386–391.

TAUSON, A., 1927, Die Spermatogenese bei Asplanchna intermedia Huds. *Zeits. Zellforsch. u. mikr. Anat.*, **4,** 652–681.

TAYLOR, W. R., 1924 *a*, The smear method for plant cytology. *Bot. Gaz.*, **78,** 236–238.

TAYLOR, W. R., 1924 *b*, Cytological Studies on Gasteria I. Chromosome Shape and Individuality. *Amer. J. Bot.*, **11,** 51–59.

TAYLOR, W. R., 1925 *a*, The Chromosome Morphology of Veltheimia, Allium and Cyrtanthus. *Amer. J. Bot.*, **12,** 104–115.

TAYLOR, W. R., 1925 *b*, Cytological Studies on Gasteria II. A Comparison of the Chromosomes of Gasteria, Aloë and Haworthia. *Amer. J. Bot.*, **12,** 219–223.

TAYLOR, W. R., 1925 *c*, Chromosome constrictions as distinguishing characteristics in plants. *Amer. J. Bot.*, **12,** 238–244.

TAYLOR, W. R., 1928, General Botanical Microtechnique (*Microscopical Technique*, ed. C. E. McClung). (Paul Hoeber.)

TAYLOR, W. R., 1931, Chromosome Studies on Gasteria III. Chromosome structure during microsporogenesis and the postmeiotic mitosis. *Amer. J. Bot.*, **18,** 367–386.

THOMPSON, W. C., 1926 *a*, Chromosome behavior in a cross between wheat and rye. *Genetics*, **11,** 317–332.

THOMPSON, W. C., 1926 *b*, Chromosome Behaviour in Triploid Wheat Hybrids. *J. Genet.*, **17,** 43–48.

THOMPSON, W. C., 1930, Shrivelled endosperm in species crosses in wheat, its cytological causes and genetical effects. *Genetics*, **15,** 99–113.

THOMPSON, W. C., 1931, Cytology and Genetics of Crosses between Fourteen- and Seven-Chromosome Species of Wheat. *Genetics*, **16,** 309–324.

THOMSEN, M., 1927, Studien über die Parthenogenese bei einigen Cocciden und Aleurodiden. *Zeits. Zellforsch. u. mikr. Anat.*, **5,** 1–116.

*TIMOFÉEFF-RESSOVSKY, N. W., 1931, Die bisherigen Ergebnisse der Strahlengenetik. *Ergeb. midiz. Strahlenforsch.*, **5,** 131–228.

TISCHLER, G., 1918, Untersuchungen über den Riesenwuchs von *Phragmites communis* var. *pseudodonax*. *Ber. Deuts. Bot. Ges.*, **36,** 549–558.

*TISCHLER, G., 1922, Allgemeine Pflanzenkaryologie. *Hb. d. Pflanzenanatomie* II., Berlin.

*TISCHLER, G., 1927, Pflanzliche Chromosomenzahlen. *Tabulae Biol. Period.*, **4,** 1–83.

TISCHLER, G., 1928, Über die Verwendung der Chromosomenzahl für phylogenetische Probleme bei den Angiospermen. *Biol. Zbl.*, **48,** 321–345.

TISCHLER, G., 1929, Verknüpfungsversuche von Zytologie und Systematik bei den Blütenpflanzen. *Ber. Deuts. Bot. Ges.*, **47,** (30)–(49).

TISCHLER, G., 1930, Über die Bastardnatur des persischen Flieders. *Zeits. f. Bot.*, **23,** 150–162.

*TISCHLER, G., 1931, Pflanzliche Chromosomenzahlen. *Tab. Biol. Period.*, **7,** 109–226.

TORVIK, M. M., 1931, Genetic Evidence of biparental males in Habrobracon. *Biol. Bull.*, **61,** 139–156.

TRANKOWSKI, D. A., 1931, Zytologische Beobachtungen über die Entwicklung der Pollenschläuche einiger Angiospermen. *Planta*, **12,** 1–18.

TSCHERMAK, E., 1930, Neue Beobachtungen am fertilen Artbastard Triticum turgidovillosum. *Ber. Deuts. Bot. Ges.*, **48,** 400–407.

TSCHERMAK, E. v. and BLEIER, H., 1926, Über fruchtbare Ægilops-Weizenbastarde. *Ber. Deuts. Bot. Ges.*, **44,** 110–132.

TUAN, H–C., 1931, Unusual Aspects of Meiotic and Post-Meiotic Chromosomes of *Gasteria*. *Bot. Gaz.*, **92,** 45–65.

TURESSON, G., 1930, Studien über *Festuca ovina* L. II. Chromosomenzahl und Viviparie. *Hereditas*, **13,** 177–184.

TURESSON, G., 1931, Über verschiedene Chromosomenzahlen in *Allium schoenoprasum* L. *Bot. Not.* (*Lund*), 1931, 15–20.

Tuschnjakowa, M., 1929 *a*, Embryologische und Zytologische Beobachtung über Listera ovata (Orchidaceae). *Planta*, **7**, 29–44.

Tuschnjakowa, M., 1929 *b*, Untersuchungen über die Kernbeschaffenheit einiger diözischer Pflanzen. *Planta*, **7**, 427–443.

Tuschnjakowa, M., 1930, Über einen eigenartigen dreifachen Chromosomenkomplex in der Reduktionsteilung der Pollenmutterzellen von Humulus Japonicus. S. et Z. *Planta*, **10**, 597–610.

Vandel, A., 1927 *a*, La Cytologie de la Parthenogénèse Naturelle. *Bull. Biol.*, **61**, 93–125.

Vandel, A., 1927 *b*, Gigantisme et Triploidie chez l'Isopode *Trichoniscus* (*Spiloniscus*) *provisorius* Racovitza. *C. R. Soc. Biol.*, **97**, 106–108.

Vilmorin, R. de, 1929, Etude cytologique du *Solanum Commersonii*. *Arch. d'Anat. micr.*, **25**, 382–387.

Vilmorin, R. de, and Simonet, M., 1928, Recherches sur le Nombre des Chromosomes chez les Solanées. *Proc. V. Int. Kong. Vererb.*, **2**, 1520–1536.

Vries, H. de, 1918, Mass Mutations and Twin Hybrids in Oenothera grandiflora Ait. *Bot. Gaz.*, **65**, 377–422.

Vries, H. de, 1919, Oenothera rubrinervis, a half mutant. *Bot. Gaz.*, **67**, 1–26.

Wakayama, K., 1930, Contributions to the Cytology of Fungi. I. Chromosome Number in Agaricaceæ. II. Cytological studies in Morchella deliciosa. *Cytologia*, **1**, 369–388, **2**, 27–36.

Warth, G., 1925, Zytologische, histologische und stammesgeschichtliche Fragen aus der Gattung Fuchsia. *Z.I.A.V.*, **38**, 200–257.

Watkins, A. E., 1924, Genetic and Cytological studies in Wheat, I. *J. Genet.*, **14**, 129–171.

Watkins, A. E., 1930, The Wheat Species: A Critique. *J. Genet.*, **23**, 173–263.

Watkins, A. E., 1932, Hybrid Sterility and Incompatibility. *J. Genet.*, **25**, 125–162.

Webber, J. M., 1930, Interspecific Hybridization in Nicotiana XI. The cytology of a sesquidiploid hybrid between Tabacum and sylvestris. *Univ. Calif. Pub. Bot.*, **11**, 319–354.

Wedekind, G., 1927, Zytologische Untersuchungen an Barrouxia Schneideri (Gametenbildung, Befruchtung und Sporogonie) zugleich ein Beitrag zum Reduktionsproblem (Coccidienuntersuchungen I). *Zeits. Zellforsch. u. mikr. Anat.*, **5**, 505–595.

Weinedel-Liebau, F., 1928, Zytologische Untersuchungen an *Artemisia*-Arten. *Jahrb. wiss. Bot.*, **69**, 636–686.

Weismann, A., 1892, *Das Keimplasma*: eine Theorie der Vererbung. Jena.

Wenrich, D. H., 1916, The Spermatogenesis of Phrynotettix magnus, with special reference to synapsis and the individuality of the chromosomes. *Bull. Mus. Comp. Zool. Harvard*, **60**, 57–135.

Wenrich, D. H., 1917, Synapsis and chromosome organisation in Chorthippus (Stenobothrus) curtipennis and Trimeropteris suffusa (Orthoptera). *J. Morphol.*, **29**, 471–516.

Werner, O. S., 1931, The Chromosomes of the Domestic Turkey. *Biol. Bull.*, **61**, 157–164.

Wettstein, F. v., 1920, Künstliche haploide Parthenogenese bei *Vaucheria* und die geschlechtliche Tendenz ihrer Keimzellen. *Ber. Deuts. Bot. Ges.*, **38**, 260–266.

WETTSTEIN, F. v., 1924, Morphologie und Physiologie des Formwechsels der Moose auf genetische Grundlage, I. *Z.I.A.V.*, **33,** 1–236.

WETTSTEIN, F. v., 1927, Die Erscheinung der Heteroploidie, besonders im Pflanzenreich. *Ergeb. Biol.*, **2,** 311–356.

WETTSTEIN, F. v., 1928 *a*, Über plasmatische Vererbung und über das Zusammenwirken von Genen und Plasma. *Ber. Deuts. Bot. Ges.*, **46** (32)–(49).

WETTSTEIN, F. v., 1928 *b*, Morphologie und Physiologie des Formwechsels der Moose. II. *Biblioth. Genet.*, **10,** 1–216.

WHITING, P. W., 1923, Further Points on the Relation of Cytology and Genetics. *J. Hered.*, **14,** 116–118.

WHITNEY, D. D., 1929, The Chromosome cycle in the rotifer Asplanchna amphora. *J. Morphol.*, **47,** 415–433.

WHYTE, R. O., 1930, Sterility and Floral Abnormality in the Tetraploid *Saxifraga potternensis. J. Genet.*, **23,** 93–122.

WILSON, E. B., 1905 *a*, Studies on Chromosomes I. The Behavior of the Idiochromosomes in Hemiptera. *J. Exp. Zool.*, **2,** 371–405.

WILSON, E. B., 1905 *b*, The Paired Microchromosomes, Idiochromosomes and Heterotropic Chromosomes in Hemiptera. *J. Exp. Zool.*, **2,** 507–545.

WILSON, E. B., 1909, Studies on Chromosomes V. The Chromosomes of Metapodius. A Contribution to the Hypothesis of the Genetic Continuity of the Chromosomes. *J. Exp. Zool.*, **6,** 147–205.

WILSON, E. B., 1911, Studies on the Chromosomes VII. A Review of the Chromosomes of Nezara; with some more general considerations. *J. Morphol.*, **22,** 71–110.

WILSON, E. B., 1912, Studies on Chromosomes VIII. Observations on the maturation phenomena in certain hemiptera and other forms, with considerations on synapsis and reduction. *J. Exp. Zool.*, **13,** 345–448.

WILSON, E. B., 1914, The Bearing of Cytological Research on Heredity. *Proc. Roy. Soc.* B, **88,** 333–352.

WILSON, E. B., 1925, *The Cell in Development and Heredity.* New York. (Macmillan.)

WINGE, Ø., 1917, The chromosomes. Their numbers and general importance. *C.R. Trav. Carlsb.*, **13,** 131–275.

WINGE, Ø., 1922 *a*, A Peculiar Mode of Inheritance and its Cytological Explanation. *J. Genet.*, **12,** 137–144.

WINGE, Ø., 1922 *b*, Crossing over between the X- and the Y-chromosome in *Lebistes. J. Genet.*, **13,** 201–217.

WINGE, Ø., 1923 *a*, One-sided Masculine and Sex-linked Inheritance in *Lebistes reticulatus. J. Genet.*, **12,** 145–162.

WINGE, Ø., 1923 *b*, On sex chromosomes, sex-determination and preponderance of females in some dioecious plants. *C. R. Trav. Carlsb.*, **15** (5), 1–25.

WINGE, Ø., 1924, Zytologische Untersuchungen über Speltoide und andere mutantenähnliche Aberranten beim Weizen. *Hereditas*, **5,** 241–286.

WINGE, Ø., 1925, Contributions to the knowledge of chromosome numbers in plants. *Cellule*, **35,** 303–324.

WINGE, Ø., 1929, On the nature of the sex chromosomes in Humulus. *Hereditas*, **12,** 53–63.

WINGE, Ø., 1930, On the occurrence of *XX* males in *Lebistes*, with some remarks on Aida's so-called " non-disjunctional " males in *Aplocheilus. J. Genet.*, **23,** 69–76.

WINGE, Ø., 1931, X- and Y-Linked Inheritance in *Melandrium. Hereditas,* **15,** 127–165.

DE WINIWARTER, H., 1931, Evolution de l'Hétérochromosome chez Tettigonia (Decticus) albifrons (Fab.). *Arch. d. Biol.*, **42,** 201–228.

WINKLER, H., 1916, Über die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. *Zeits. f. Bot.*, **8**, 417–531.

WINKLER, H., 1921, Über die Entstehung von genotypischer Verschiedenheit innerhalb einer reinen Linie (Report of paper read to Deuts. Ges. f. Vererb.). *Z.I.A.V.*, **27**, 244–245.

WITSCHI, E., 1924, Die Entwicklung der Keimzellen der Rana temporaria L. I. Urkeimzellen und Spermatogenese. *Zeits. Zell. u. Geweb.*, **1**, 523–561.

*WITSCHI, E., 1929, Bestimmung und Vererbung des Geschlechtes bei Tieren. *Hdb. d. Vererbungswiss.*, **2**.

WOLFSON, A. M., 1925, Studies on aberrant forms of *Sphærocarpos Donnellii. Amer. J. Bot.*, **12**, 319–326.

WOLTERECK, R., 1898, Zum Bildung und Entwicklung des Ostrakoden-Eies. Kerngeschichtliche und biologische Studien an parthenogenetischen Cypriden. *Zeits. Wiss. Zool.*, **64**, 596–623.

WOODRUFF, L. L., and ERDMAN, R., 1914, A normal periodic reorganisation process without cell fusion in Paramœcium. *J. Exp. Zool.*, **17**, 425–502.

WOOLSEY, C. I., 1915, Linkage of Chromosomes correlated with reduction in number among the species of a genus, also within a species of the Locustidæ. *Biol. Bull.*, **28**, 163–186.

YAMAHA, G., 1926, Über die Lebendbeobachtung der Zellstrukturen, nebst dem Artefactproblem im Pflanzenzytologie. *Bot. Mag. Tokyo*, **40**, 172–197.

YAMAHA, G., 1927, Experimentelle zytologische Beiträge, III. Mitteilung. Über die Wirkung einiger Chemikalien auf die Pollenmutterzellen von *Daphne odora*, Thunb. *Bot. Mag. Tokyo*, **41**, 181–211.

YAMAHA, G., and SINOTO, Y., 1925, On the Behaviour of the Nucleolus in the Somatic Mitosis of Higher Plants, with Micro-chemical Notes. *Bot. Mag. Tokyo*, **39**, 205–226.

YAMANOUCHI, S., 1908, Apogamy in Nephrodium. *Bot. Gaz.*, **45**, 289–318.

YAMANOUCHI, S., 1912, The Life History of Cutleria. *Bot. Gaz.*, **54**, 441–502.

YARNELL, S. H., 1929, Meiosis in a triploid Fragaria. *Proc. Nat. Acad. Sci.*, **15**, 843–844.

YARNELL, S. H., 1931 *a*, Genetic and Cytological Studies on *Fragaria. Genetics*, **16**, 422–454.

YARNELL, S. H., 1931 *b*, A study of certain Polyploid and Aneuploid Forms in *Fragaria. Genetics*, **16**, 455–489.

YASUI, K., 1921, On the Behavior of Chromosomes in the Meiotic Phase of some Artificially Raised *Papaver* Hybrids. *Bot. Mag. Tokyo*, **35**, 154–168.

YASUI, K., 1927, Further Studies on Genetics and Cytology of Artificially Raised Interspecific Hybrids of *Papaver. Bot. Mag. Tokyo*, **41**, 235–261.

YASUI, K., 1931, Cytological Studies in Artificially Raised Interspecific Hybrids of *Papaver* III. Unusual Cases of Cytokinesis in Pollen Mother-Cells in an F_1 Plant. *Cytologia*, **2**, 402–419.

ZIRKLE, C., 1928, Nucleolus in root tip mitosis in Zea mays. *Bot. Gaz.*, **86**, 402–418.

ZIRKLE, C., 1931, Nucleoli of the Root Tip and Cambium of *Pinus Strobus. Cytologia*, **2**, 85–105.

SUBJECT INDEX

Including names of authors not mentioned in the Bibliography. The letter (G) indicates that a term is defined in the Glossary.

ABRAXAS, 463
Acarina, 418, 465
Aconitum, 35, 216, 217
Acrididæ, 80, 81, 460
Acridium, 153, 274
Acrocladium, 206
Actinophrys, 6, 13
  meiosis, 92, 108
adaptation, 460, 472, 483
  v. genotypic control,
    natural selection.
adjustment, 237
Ægilops, 59, 151, 152, 153, 163, 186, 354
Ægilotricum, 173, 176, 195, 209
Æsculus carnea, 46, 59, 217 *et sqq.*
affinity, 489
  v. attraction,
    differential affinity,
    pairing.
    terminal, 332 *et sqq.*
Agaricaceæ, 85
Aggregata, 6, 14, 26, 28, 44, 50
  chiasmata, 108
  chromosome
    contraction, 300, 453
    permanence, 43 *et sqq.*
  life cycle, 6, 457
  segregation, 248
Alchemilla, 420, 434
Aleurodes, 418
Algæ, 6, 437, 458
allelomorphs, 246, 456
Allium, 20 (Fig. 2), 38, 39, 71, 208, 210
  nutans, 120
  odorum, 346, 421 *et sqq.*, 441, 444, 470
  roseum, 445 *et sqq.*
  Schœnoprasum, 200
Allolobophora, 109
(G) allopolyploid, 169
(G) allosyndesis, 183
Alnus, 199
Aloë purpurascens, 30, 153
  saponaria, 37
Alstroemeria, 39
(G) alternation of generations, 6, 417 *et sqq.*
Alydus, 45, 70, 91, 109, 135, 333, 349, 389
Amblystegium, 201
(G) amitosis, 28, 29
Amœba, 29, 108
  terricola, 18
  verrucosa, 18
Amorpha, 162, 164
(G) amphimixis, 455 *et sqq.*
(G) anaphase
  forces, 340
  meiosis, 90, 91, 110 *et sqq.*, 270
  mitosis, 26
  multivalents, 124, 340
Anasa, 333, 389
(G) anaschistic
Ancyracanthus, 8, 46, 384
(G) androgenesis
Anemone, 94, 109, 211, 334
(G) aneuploid
Angiostomum, 361
Anisolabis, 381, 389
Annelida, polyploidy, 65, 446
Antennaria, 420, 435, 445
antheridia, 419
antherozoid, 7
Anthoxanthum odoratum, 109, 111, 150, 152
Antirrhinum, 82
Aphides, 361, 384, 470
Aphis, 334, 431, 469
Apis (Bee), 16, 56, 418, 439, 467
Aplocheilus, 464
(G) apogamy, 417 *et sqq.*
(G) apomixis, 4, 416 *et sqq.*, 469 *et sqq.*
  in *Rosa*, 368

(G) apospory, 417 *et sqq.*, 469 *et sqq.*
  gives tetraploids, 65
Apotettix, 251, 432, 441, 470, 474
archegonia, 419
Arphia, 153, 351
artefact, 488
Artemia, 205, 431–2, 446
Artemisia nitida, 151, 420, 432, 445
Ascaris
  aggregation of chromosomes, 55
  chromosome numbers, 84, 85
  diminution, 56
  fertilisation, 9
  lack of precocity, 346
  resting nucleus, 43
  triploid embryos, 40
Ascomycetes, 6, 456
asexual reproduction, 4, 423
Asilus, 301, 379
Asplanchna, 418, 439
asynapsis. *v. Zea.*
(G) atelomitic
Athyrium, 419
(G) attachment. *v.* spindle attachment.
  of chromosomes. *v.* fusion.
  granules, 91
  at meiosis, 98, 104 *et sqq.*
    v. polar granules.
attraction, 218, 300 *et sqq.*
Aucuba japonica
  constrictions, 35, 37
  interchange, 149, 150, 152
  inversion, 72
  lagging, 111
  lateral chiasmata, 138
  precocity, 348
  terminalisation, 109, 321
Aulacantha scolymantha, 37, 85
autopolyploid, 169
  reduced fertility, 178
  species, 198 *et sqq.*
(G) autosomes, 391 *et sqq.*, 462
(G) autosyndesis, 182 *et sqq.*, 209, 224
Avena, 152, 184, 197, 200, 353

BACILLUS, 432, 452
Bacteria, 2, 451, 456, 464
(G) balance, 59, 172, 180, 224 *et sqq.*, 480 *et sqq.*
  secondary, 239
  and sex, 391 *et sqq.*, 462 *et sqq.*
Balanophora, 420
Barrouxia schneideri, 108
(G) basic number, 61, 77
Basidiomycetes, 3, 6, 9
  homothallic and heterothallic, 9, 15
  life cycle, 458
  meiosis and parthenogenesis, 438
  segregation, 248
Bateson, William, 169, 484
bee. *v. Apis.*
Bellevalia romana, 30, 31, 93
Belostoma, 91
Benacus, 487
Berg, 480
Beta, 62, 191
Betula, 190
Biscutella, 60, 212
(G) bivalent, 90, 104 *et sqq.*
  unequal, 153, 273 *et sqq.*
Blaps, 383
blepharoplast, 7
Bombinator igneus, 108
Bombyx, 134
Bonellia viridis, 13
Bougainvillea glabra, 153
(G) bouquet stage, 92
brachymeiosis, 375, 456
Brachystola, 152, 351
Brassica
  hybrids, 191 *et sqq.*, 195, 225
  syndiploidy, 63
  tetraploid, 176
  univalents, 359
    v. also *Raphanus.*
brazilin, 492
Briza media, 151
Brochymene, 387
Bromus erectus, 197, 198, 356
Bryophyta, 6, 248, 378, 416, 429, 464
Bryum, 466

CALLITRICHE, 86, 211
Camarophyllus, 424, 431, 438
Cambarus virilis, 37, 85
Camnula, 351
Campanula persicifolia
  interchange, 141 *et sqq.*
  interlocking, 271 *et sqq.*
  multiple chiasmata, 117
  parthenogenesis, 426
  segregation of rings, 340
  terminalisation, 102, 312 *et sqq.*, 407
  tetraploid, 178

Canna, 118, 150, 160, 164, 178, 200
Cannabis sativa, 13
Cardamine pratensis, 80, 197
Carnoy's fixative, 491
Cassia, 211
Celeris, 162
(G) cell, 2 *et sqq.*; size, 205 *et sqq.*
Celosia, 193
centrifuging, 16, 17, 46
(G) centrosome, 7, 22, 23, 28
centrosphere, 23
Cepea, 251
Ceresa, 388
Chara, 416, 424, 439 *et sqq.*, 446
Charophyta, 6
(G) chiasma
  adaptation, 459
  breakage, 256 *et sqq.*, 310, 311, 316
  causation, 289
  classification, 309
  compensating, 112, 132, 286, 321, 329
  and crossing over, 252 *et sqq.*
  definitions, 95, 256
  distribution, 285
  in fragments, 136
  frequency, 98, 122, 127, 157, 277, 286
  function, 123, 127
  genetical significance, 254
  inference, 221, 487
  interference, 95, 283
  interstitial, 103, 124, 143
  lateral, 132, 134 *et sqq.*
  localisation, 98, 156, 394 *et sqq.*
  morphology, 89, 90, 95
  multiple, 116, 309, 329 *et sqq.*
  origin of, 312, 313, 317, 333, 455
    in polypoids, 116 *et sqq.*
  suppression, 283, 351
  terminal, 103, 160, 258, 316; theory of, 328
  terminalisation. *v.* terminalisation.
(G) theory of pairing, 126, 157, 260, 283
  variation in frequency, 165
(G) chiasmatype hypothesis, 113, 252 *et sqq.*
Chilodon, 18
(G) chimæra, 73, 425
  v. mosaic.
Chlamydophrys Schaudinni, 18
Chloëaltis, 80
Chlorophyceæ, 2, 6
chloroplasts, 205
Chondrilla, 420, 444
(G) chondriosomes, 2
Chorthippus, 80
  v. Stenobothrus.
Chromacris miles, 108
(G) chromatid
  association, 103
  attraction between ——s, 303
  crossing-over between ——s, 278
  definition, 21
  diameter, 50
  at diplotene, 90, 95
  interlocking, 271, 273
  at interphase, 91
  segregation, 279
  separation, 110, 270
  spiral structure, 30 *et seq.*, 487
  at terminal chiasmata, 317
(G) chromatin, 291
(G) chromiole
(G) chromomeres, 21, 22, 31, 88, 116, 230, 342, 488
(G) chromonema, 42
(G) chromosome, 2, 5, 13
  accessory materials, 59, 270, 290, 453
  affinities, 116
  aggregation, 55
  breadth, 50, 53
  bulk, 50, 52
  constants, 50
(G) contraction, 30, 94, 113
    at anaphase, 26, 342
    origin, 453
    at prophase, 30, 303; of meiosis, 93, 100
    at second division, 91
  division, 48, 300 *et sqq.*, 487
  maps, 286
  numbers, 85, 213
  origin, 452
  pellicle, 270, 290
  range of size, 84, 85
  repulsions and attractions between, 301 *et sqq.*, 326 *et sqq.*
(G) sets, 169, 175, 178
  supernumerary, 135
  theory of heredity, 227 *et sqq.*, 499

chromosome, as unit, 297, 403
Chrysanthemum
  hybrids, 161, 190 *et sqq.*, 354
  syndiploidy, 63
Ciliata, 6
Circotettix verruculatus
  chromosome form, 80
  terminalisation, 109, 313, 314
  unequal bivalents, 153, 247, 274, 313
Citrus Limonum, 64, 200, 423
Cladocera, 470, 474
Cladophora, 6, 109
Clarkia elegans, 151
clonal species, 202, 472
clones, 4, 11
Coccidæ, 372, 418, 439
Cocconeis, 424, 432
Cochlearia, 203
Coleoptera, 384, 387
Coleotrype natalensis, 83
Commelina cœlestis, 83
competition
  among embryos, 424
    embryo-sacs, 400
    gametes and zygotes, 232 *et sqq.*
    pairing chromosomes, 189, 241
complement (of chromosomes), 2, 40, 231
complex, 398 *et sqq.*
conjugate nuclei, 9
(G) constrictions
  interpretation, 487
  occurrence, 34 *et sqq.*
  origin of, 76
  variation, 51, 53 *et sqq.*
Cratægus, 194, 200
Crepis
  apomixis in, 446
  autosyndesis, 186
  cell size, 205
  crossing-over in hybrids, 264
  hybrids, 190 *et sqq.*
  mitotic chromosomes, 37
    in hybrids, 46, 54
  spiral structure, 32
  structural changes, 69 *et sqq.*
 acuminata, 446
 artificialis, 190, 226
 biennis, 201, 203
 Bungei, 211
 capillaris
   differential affinity, 182, 190
Crepis capillaris—(*contd.*).
   failure of pairing, 352
   haploid, 62, 363, 426
   hybrids, 153, 154, 163
   polyploid series, 61
   progeny of triploid, 233
   size of chromosomes, 85
   tetraploids, 170 *et sqq.*, 179 *et sqq.*
   triploid, 199
 ciliata, 203
 dioscoridis (deficiency), 57
 tectorum
   analysis of variation, 72
   pentaploid, 201, 206
   ring chromosome, 39, 66
   translocation, 57
Crocus, 216
(G) crossing-over, 250 *et sqq.*, 450
  with autosyndesis, 172
  cause of, 288, 455
  in complex heterozygotes, 405 *et sqq.*
  in haploids, 242
  in hybrids, 181
  "illegitimate," 242
  of lethals, 411
  with non-reduction, 473
  in *Œnothera*, 407 *et sqq.*
  in polyploids, 278
  in sex chromosomes, 376, 380, 394, 461
  at successive chiasmata, 113
  suppression in the heterozygous sex, 394
  theory, 228, 250 *et sqq.*
  unequal, 245
Crustacea, 417, 446
Cryptobranchus, 46
Cupressus, 81
Cutleria, 425
Cyanophyceæ, 2
Cyanotis Zenonii, 37, 83
  somaliensis, 83
Cycas revoluta, 81, 111, 355
Cyclops, 45
Cynips, 431
Cypris, 432
(G) cytokinesis
  failure of, 360
(G) cytoplasm, 2 *et sqq.*, 8
  inheritance, 481

DAHLIA, 111, 218, 222
  Merckii, 60, 224 *et sqq.*, 481

Dahlia variabilis, 109
Daphnia, 417, 446
Darwin, Charles, 480, 483 *et sqq.*
Dasychira pudibunda, 81, 84
Datura Stramonium
  cell size, 205
  chiasmata, 157; multiple, 117
  constrictions, 38
  doubling in haploid, 62
  figure-of-eight, 267
  fragmentation, 69, 135
  haploid, 363, 426
  interchange, 141, 404
  interlocking, 273
  monosomics, 230
  multiple chiasmata, 117
  multivalents, 117 *et sqq.*, 126
  non-reduction, 362
  pollen abortion, 235
  polyploid and polysomic forms, 60, 67
  progeny of unbalanced forms, 233 *et sqq.*
  reduplication, 139
  syndiploidy, 63
  terminalisation, 109, 321
  tetraploid, 169, 178
deficiency, 48, 67, 68, 230 *et sqq.*, 261, 481
deletion. *v.* deficiency.
Dendrocœlum lacteum, 30, 92, 108
Diabrotica, 135
(G) diakinesis, 89, 90, 100, 337
Dianthus, 177, 190, 211
(G) diaschistic
Dicranura, 134, 155
(G) didiploid
(G) differential affinity, 138, 171, 182 *et sqq.*, 396
differentiation
  of cells, 3 *et sqq.*
  of chromosomes, 156, 180, 209, 211, 243, 477, 478
  of genes, 45 *et sqq.*, 159, 227, 245, 451
  of sexes, 13, 376, 390, 460
diffuse stage, 92, 487
Digitalis
  autosyndesis, 190 *et sqq.*
  haploid parthenogenesis, 184, 204, 426
  hybrids, 161 *et sqq.*, 354
  non-reduction, 362
  origin of tetraploid, 176
Digitalis—(*contd.*).
  tetraploid, 171
(G) diminution, 19, 243
(G) diploid, 5, 454
  v. also haploid and polyploid.
(G) diplophase, 5, 9, 376, 458
(G) diplotene, 89, 90, 95
Diptera, 7, 218
discontinuity, 480, 484
(G) disjunction. *v.* anaphase segregation.
Dissostiera, 153
division. *v.* mitosis, meiosis and chromosome.
Dorstenia, 355
doubling (of chromosome number), 61 *et sqq.*, 425
Draba, 211
Drosera
  chiasmata, 109
  failure of reduction, 362
  hybrid, 188, 193
  capensis, 85
Drosophila
  chromosome complements, 82
  sex chromosomes, 379
  somatic pairing, 220
  melanogaster
    attached X, 68, 70
    attached Y, 68, 71
    cell-size, 207
    chiasmatype theory, 253
    chromosome maps, 80, 277; size, 85
    crossing-over, 277 *et sqq.*; in male, 284, 395
    elimination of chromosomes, 56, 58
    gene differences, 131
    haplo-IV, 60
    haploid mosaic, 465
    interchange, 151, 409
    mosaics, 10, 58
    polysomy, 66
    tetraploidy, 65
    triploid, 199, 205
    unbalanced forms, 230 *et sqq.*, 391
  obscura, 80, 281
  simulans, 393
  willistoni, 288
Drosophyllum lusitanicum, 85
Dytiscus, 19
duplication. *v.* reduplication.
(G) dyad

ECHINICERYA, 418
Echinoderms, 62, 63, 230, 416, 425, 442
Ectocarpus, 15
egg, 7, 232 *et sqq.*, 416 *et sqq.*
Elatostema, 420, 431, 470
elimination
  of chromosomes, 49, 56
  of gametes, 233 *et sqq.*
  of zygotes, 233 *et sqq.*
    v. diminution.
Elodea, 386
(G) embryo sac, 10, 231
  in apomixis, 420 *et sqq.*
  in *Rosa*, 369 *et sqq.*
Empetrum, 65, 226, 386
Enchenopa, 350, 387
endosperm, 10, 48, 421, 424, 428
environment, 11 *et sqq.*
Ephedra, 81, 108
epigenesis, 237
Epilobium, 363, 481
equational chiasma, 255, 257; split, 252 *et sqq.*
(G) ergastic
Erigeron, 420
Erophila, 211
Eucharidium concinnum, 151
Euchlæna, 426
  v. Zea.
Eucomis bicolor, 84
Euglypha, 18, 27, 28, 37
Eumeces latiscutatus, 84, 108
Eupatorium, 445
Euphorbia, 208, 222
evolution, 245, 391 *et sqq.*, 448 *et sqq.*

(G) FACTOR
(G)   balanced lethal, 400
(G)   lethal, 394, 400, 411
female, 7
  super-female, 68
(G) fertilisation, 5
  in apomixis, 421, 424, 430, 441
  discovery, 87
  double, 10
  errors of, 429
  in haploid parthenogenesis, 425
fertility, 143, 170 *et sqq.*, 178 *et sqq.*, 198 *et sqq.*, 209
  of haploids, 365
  in *Œnothera*, 399
  of triploids, 232 *et sqq.*
Festuca
  chiasma frequency, 351
  hybrid, 163, 351
  terminalisation, 109
  triploid, 147, 176
  vivipary, 423, 446
Filaria, 8, 46
first division, 88 *et sqq.*
Fischer, 486
fishes (*v.* also *Lebistes*), 464
fixation, 32, 42, 54, 486 *et sqq.*, 491 *et sqq.*
Flagellata, 4, 6
flaking, 242
Flemming's fixative, 492
Forficula, 109, 153, 321, 381, 389
Fourcroya altissima, 84
Fragaria,
  hybrids, 162, 190
  parthenogenesis, 428
  sex chromosomes, 378, 386
  tetraploid, 176
  triploid, 147, 152
fragmentation, 67 *et sqq.*
  cause of, 242
  heterozygotes, 132
  occurrence, 481
fragments
  division, 304
  non-disjunction, 66
  pairing of, 136
  precocity, 350
  survival of, 73 *et sqq.*
  terminalisation, 313
  transmission, 234
Fritillaria imperialis
  chiasmata, 98, 101, 283
  fragmentation, 70, 135
  fragments, 350
  terminalisation, 313 *et sqq.*
 Meleagris
    anaphase, 270
    compensating chiasmata, 329
    distal precocity, 348
    localisation, 98, 394
 pudica
    chromosome fragmentation, 80
    triploid, 200
 ruthenica
    chiasmata, 99
    chromosome fusion, 80
fruits, 206
Fucus, 6

Funaria, 201, 205 *et sqq.*, 248, 251, 363, 442, 474, 481
Fungi, 424, 437, 456 *et sqq.*
fusion
    conditions of, 73
    evidence of, 67 *et sqq.*
    heterozygotes, 132
    of sex chromosomes, 383 *et sqq.*
    and species, 481

GAGEA, 363
Galeopsis, 123, 176, 192, 217
Galtonia, 32
(G) gametes, 2, 4 *et sqq.*, 230 *et sqq.*, 417
    unreduced, 358, 411
(G) gametophytes, 6, 229, 419
Gasteria, 32, 113
(G) gene, 67, 159, 228, 237, 241, 244, 296, 450 *et sqq.*, 478 *et sqq.*
generative nucleus, 7, 10
genetic property, 12, 469
    v. genotype.
(G) genome
(G) genotype, 11, 245, 448
(G) genotypic control
    of chiasma formation, 159, 283, 460
    of chromosome form, 52 *et sqq.*
    of crossing-over, 283, 394, 462
    of meiosis, 88, 439, 459
    of pairing, 161, 469
    of particular chromosomes, 156
    of spindle, 63, 64
    theory of, 449
        v. mendelian inheritance.
gentian violet, 488, 491
germ-cells. *v.* gametes.
germ-plasm, 11, 87, 470
Geum, 162
Giemsa, 488, 492
gigantism, 206 *et sqq.*
Godetia, 151
Gomphocerus maculatus, 63
Gossyparia, 349, 374
Gossypium, 226
Gregarina, 6
(G) growth, 3 *et sqq.*
Gryllus, 80, 94, 379
Gymnospermæ, 81, 416
gynandromorphs, 66

HABROBRACON, 206, 418, 439
hæmatoxylin, 488, 492
haplo-diploid sex differentiation, 206, 417, 465
(G) haploid, 5, 60, 62
    definition, 231
    derived from polyploids, 184
    meiosis in, 363, 367, 437
    at meiosis, 88, 91, 93
    origin of, 425 *et sqq.*; males, 418
haplophase, 5, 9
Hemerocallis, 117, 120, 200
Hemiptera
    haploid males, 418
    precocity, 348
    prophase of meiosis, 91, 94
    sex chromosomes, 384 *et sqq.*
heredity, 1, 10 *et sqq.*, 227 *et sqq.*
hermaphrodites, 13, 397, 418, 466
Hertwig, O., 87
Hesperotettix, 71, 133, 385
(G) heterochromosomes
(G) heterogamy, 401
(G) heteroploid
(G) heteropycnosis
    v. precocity, differential.
heterosis, 129, 456
heterothallism, 9, 14
(G) heterotypic division. *v.* first division.
(G) heterozygote, 129 *et sqq.*, 169
    complex, 376, 398
    sex, 376 *et sqq.*
(G) heterozygous sex, 129
(G) hexad
hexaploid. *v.* polyploid.
Hieracium
    apomixis, 420 *et sqq.*, 443 *et sqq.*, 469 *et sqq.*
    hybrids, 193
    suppression of meiosis, 360
    univalents, 366
(G) homeotypic division. *v.* second division.
Homo sapiens, 85, 109
(G) homogametic sex
(G) homology, 156
    change of, 182, 320
    inference, 489
    theory of, 296
    within the haploid, 241
(G) homozygote
homozygous sex, 376 *et sqq.*
Humaria rutilans, 85, 108

Humulus japonicus, 151, 379 *et sqq.*, 475
  Lupulus, 151, 381 *et sqq.*
Hyacinthus
  balance, 238
  amethystinus, 286, 460
  orientalis
    abnormal mitosis, 360
    chiasma frequency, 286
    chiasmata, 98, 108, 122
    crossing-over, 265
    diffuse stage, 94
    division of trivalents, 304
    meiosis in polyploid, 114 *et sqq.*
    nucleoli, 17
    quadrivalents, 122, 265
    qualitative differentiation, 180
    size of chromosomes, 85, 98, 122
    spiral structure, 32
    triploid, 201 ; pollen grain, 231
hybridisation, 245, 478
  and apomixis, 442 *et sqq.*, 469
  and meiosis, 456
  in *Œnothera*, 409, 412
  and parthenogenesis, 425
hybridity, 456 *et sqq.*, 469 *et sqq.*
(G) hybrids
  breeding true, 170, 371, 376, 399, 469 *et sqq.*
  classification, 130 *et sqq.*
  complex, 131
  definition, 128 *et sqq.*
  false, 426, 442
  interpretation of meiosis, 308, 312
  mendelian, 131
  numerical, 130
  pairing in, 162, 319
  structural, 130
  twin, 399
  undefined, 130, 155, 160 *et sqq.*
    v. heterozygote.
Hydrilla, 199
hydrogen-ion concentration, 31, 42, 53
Hymenoptera, 62, 361, 418, 439, 465
Hypericum punctatum, 151

ICERYA purchasi, 21, 295, 367, 375, 418, 430, 439
Iguanidæ, 63
illegitimate crossing-over, 242 *et sqq.* ; pairing, 197
incompatibility, 15
individuality of the chromosomes, 41
Infusoria, 16, 29
inheritance (of ring-formation), 144, 404
(G) interchange, 67 *et sqq.*
  cause of, 408
  in haploids, 242
  heterozygotes, 140 *et sqq.*, 282
  in *Œnothera*, 405 *et sqq.*
  with sex chromosomes, 381
    v. crossing-over.
(G) interference
  at diplotene (between chiasmata), 95, 283, 285
  genetic, 252
  at zygotene (between chromosomes), 157, 197, 280
interlocking, 157, 256, 270 *et sqq.*
(G) interphase (in meiosis), 32, 90, 113
interpretation, 486
intersexes, 391 *et sqq.*
(G) inversion, 67, 281, 481
Iris, 200
irradiation, 48
  v. X-rays.
(G) isogamy

JAMAICANA, 134
Johannsen, W., 244

(G) KARYOKINESIS
(G) karyolymph
(G) karyomere (nuclear compartment), 45, 91
(G) karyosphere, 94
Kern-plasma ratio, 17
Kniphofia, 64, 108, 165, 324, 329, 341, 346, 356, 360

LABIDURA bidens, 153
Lacertilia, 63
Lachenalia, 37, 111
lagging, 111
Lamarckianism, 484 *et sqq.*
Lamium, 193
Lathyrus, 32, 258, 322
Lebistes, 251, 387 *et sqq.*, 397
Lecanium, 372, 431, 432
Leguminosæ, 277
Lens, 426

Lepidoptera, 92, 100, 109, 161, 350, 378
Leptophyes, 379
(G) leptotene, 88, 91
Leptynia attenuata, 108, 385, 388
lethal, 235; factors, *v*. factors.
life cycle, 3 *et sqq.*, 11, 417 *et sqq.*; origin of, 457 *et sqq.*
Liliaceæ, 66, 277, 460
Lilium, 30, 32, 322
  tigrinum, 118
linear arrangement, 47, 228, 453
  sequence, 182 *et sqq.*, 243
(G) linin
linkage
  of chromosomes
    v. ring-formation, interchange.
  of factors, 228, 251
    v. crossing-over.
Linum, 481
Liriope, 363
living cells, 486
Llaveia, 333, 373
(G) localisation. *v*. chiasmata.
Lolium. *v*. *Festuca*.
Lucretius, 1, 484
Lychnis, 363
Lycia, 154
Lycopodium, 7
Lycoris, 199
Lygæus, 333, 379 *et sqq.*
Lymantria dispar, 463
  monacha, 56, 384, 391
Lythrum Salicaria, 197, 212

(G) MACRONUCLEUS, 29
Macropus, 108, 379, 385
male, 7
  sex chromosomes, 376 *et sqq.*
  super, 68
Malva, 16
man, 53
  v. *Homo*.
Marsilia, 419, 431
(G) matroclinal, 178
Matthiola incana
  deficiency, 69, 230
  fragmentation, 69, 135, 242
  haploid, 363, 426
  hybridity, 131, 135
  precocity, 345
  progeny of unbalanced, 234
  reduplication, 139, 147
Matthiola incana—contd.
  secondary trisomics, 139
  terminalisation, 109
  trisomic, 120
(G) maturation
mechanics
  of anaphase movement, 26, 303
  of chromosome movement, 335
  of crossing-over, 289
  of spiralisation, 290
  of terminalisation, 325
Mecostethus
  chiasma frequency, 286
  crossing-over, 253, 265
  distal precocity, 348
  localisation, 98, 108, 157, 395
  unequal bivalents, 153, 274
  zygotene, 92, 98
(G) megaspore, 400
  v. embryo-sac.
(G) meiosis
  abnormal forms, 368 *et sqq.*
  adventitious, 367
  criterion of hybridity, 469
  definition, 88
  difference from mitosis, 307
  essentials of, 301
  forces at, 336 *et sqq.*
  form of mitosis, 19, 88
  in haploids, 363, 437
  history and theory, 294 *et sqq.*
  interpretation, 487
  irregularity, 357 *et sqq.*
  in life cycle, 5
  origin of, 455
  and segregation, 228, 247
  suppression of, 431
Melandrium, 53, 109, 386 *et sqq.*
Meleagris gallopavo, 84
mendelian inheritance, 345, 352, 367, 399, 406, 409, 430
  v. segregation.
Menexenus, 385
Mermiria, 134, 385
(G) metabolic stage. *v*. resting stage.
(G) metaphase
  of meiosis, 90, 103 *et sqq.*
  of mitosis, 22 *et sqq.*
  in polyploids, 118
Metapodius, 67, 135, 349
(G) metasyndesis
Miastor, 56
(G) micro-chromosomes, 156, 333
micro-dissection, 16, 43
(G) micronucleus, 16, 18, 29

- micro-species, 482
- (G) microspore, 9
  - *v.* pollen-grain.
- *Miltochrista miniata*, 81
- mitochondria, 8
- (G) mitosis, 2, 16 *et sqq.*, 19 *et sqq.*
  - duration of, 27
  - essentials of, 300
  - mitotic constants, 50, 303
  - origin of, 451 *et sqq.*
  - replacement by meiosis, 367
- Mollusca, 7, 13, 446
- *Monocystis magna*, 37
- (G) monoploid
- (G) monosomic, 60, 230
- *Morus*, 200
- (G) mosaics
  - in *Drosophila*, 10, 66, 228, 429
  - in *Nicotiana*, 75, 242
    - *v.* chimæras.
- mosses, 205
  - *v.* *Funaria*, Bryophyta.
- (G) mother-cell, 5, 7
- Muller, 279
- multicellular, 3
- multinucleate cells, 3, 9, 63
- multipolar mitoses, 63
- multispecific hybrids, 195
- multivalent segregation, 124, 340
- (G) multivalents, 118 *et sqq.*, 179, 318
- *Mus musculus*, 70, 111, 153, 390
  - *norvegicus*, 108
- *Muscari*, 37
  - *latifolium*, 38, 84
- mutability, 451, 456, 464
- mutation, 131, 159, 227, 228, 244, 450 *et sqq.*
  - and apomixis, 429, 443
  - through crossing-over, 241, 408 *et sqq.*, 471 *et sqq.*
  - in *Œnothera*, 399, 405
- Myxomycetes, 2

- *NAIAS marina*, 70
- *Narcissus*, 200, 356
- *Nasturtium*, 211
- *Natrix*, 350
- natural selection, 209, 239, 451 *et sqq.*, 459 *et sqq.*, 468, 475, 480
- Nematoda, 348, 384
- *Nephrodium*, 419, 420
- *Neuroterus*, 418
- Newton, Sir Isaac, 343
- *Nezara*, 379
- *Nicandra*, 109, 319
- *Nicotiana*, 109
  - cell size, 205
  - failure of reduction, 362
  - haploid, 363, 426
  - hybrids, 162 *et sqq.*
  - origin of polyploids, 173, 176
  - pentaploid, 201
  - polyploidy, 172
  - secondary balance, 240
  - *alata*, 230, 362
    - chromosome form, 80
    - triploid, 199
  - *digluta*, 174
    - cell-size, 205
    - fertility, 209
    - origin, 176
  - *Langsdorffii*
    - chromosome form, 80
    - haploid, 363, 426
  - *longiflora*, 223
  - *suaveolens*, 120
  - *Tabacum*
    - constitution, 197
    - doubling in haploid, 62
    - failure of pairing, 353
    - fragmentation, 69, 242
    - haploid, 184, 426
    - mosaic, 75
    - precocity, 348
    - secondary polyploid, 225
    - X-rayed, 67
- *Nigritella*, 446
- nomenclature, 88
  - *v.* glossary.
- nomogenesis, 480
- (G) non-disjunction, 66, 67, 126, 142, 389, 411
- *Nothoscordon*, 423
- novation, 71
- nucellar embryony, 64, 423, 443
- nucellus, 422
- (G) nuclear sap, 21
  - vesicles (karyomeres), 27
  - wall, 16, 103
- (G) nucleolus, 17 *et sqq.*, 46
  - at meiosis, 90, 487
- (G) nucleus, 2 *et sqq.*, 8, 16 *et sqq.*, 30
  - triple fusion, 10
  - volume, 100
- *Nyctereutes*, 350

- *OCHNA serrulata*, 201, 420 *et sqq.*, 431
- octoploid nuclei, 62

Œnothera
  apomixis, 443
  cell size, 205
  constrictions, 38
  crossing-over, 263 *et sqq.*, 282
  fertilisation, 10
  gene-mutation, 479
  half-mutants, 405
  haploids, 426
  hybrids, 129
  inheritance in, 399
  interlocking, 27 *et sqq.*
  lagging, 111
  meiosis, 142
  monosomic, 230
  multiple chiasmata, 117
  mutation in, 405
  non-reduction, 362
  pairing in haploid, 241, 268, 363
  permanent hybrids, 376
  polysomic, 60
  progeny of triploids, 232 *et sqq.*
  ring-formation, 296, 401, 460, 475
  size of chromosomes, 85
  telosynapsis, 296
  terminalisation, 110, 299, 320
  tetraploid, 152, 178
  triploid, 148, 199
(G) oligopyrene, 9
Oncopeltus, 379, 387
(G) oöcyte
oögenesis, 7, 94, 349
  in Coccidæ, 372
Oporabia, 162, 163
Orchis, 82
organism-as-a-whole, viii, 450
Orgya, 80, 154
Ornithogalum, 37, 84
orthogenesis, 480
(G) orthoploid
Orthoptera
  parthenogenesis, 441
  precocity, 348
  prophase of meiosis, 441
Osmunda, 92, 429

(G) PACHYTENE
  description, 90, 93
  in interchange heterozygotes, 140, 142
  misinterpretation, 294
  in polyploids, 115, 118
  in undefined hybrids, 161

(G) pairing of chromosomes
  causation of, 306
  conditions of, 125, 156 *et sqq.*
  failure of, 118 *et sqq.*, 137, 142, 160, 163, 431
  of fragments, 136 *et sqq.*
  genetical control, 345 *et sqq.*
  in hybrids, 130, 489
  illegitimate, 197
  internal, 183
  kinds of, 309
  "loose pairing," 160
  "pairing blocks," 122, 127, 182, 280
  in polyploids, 114 *et sqq.*, 182 *et sqq.*
  principles of, 125, 156 *et sqq.*
(G) secondary, 220, 339
  of sex chromosomes, 387
(G) somatic, 218
  terminal affinity, 333
  at zygotene, 88, 91
Papaver
  autosyndesis, 186, 190 *et sqq.*
  bivalents in hybrids, 160, 163
  hybrids, 190, 225
  polyploidy, 211
  unreduced gametes, 168, 362
Paracopidosomopsis, 418
Paramœcium, 6, 29
(G) parasynapsis, 295
Paratettix, 432, 441, 470
(G) parthenogenesis, 416 *et sqq.*
  diploid and haploid, 416 *et sqq.*
  following lack of reduction, 230
  male, 427, 442, 465
  origin of, 470
  in polyploids, 65, 184, 204
Pellia, 350
Pergesa, 162
Perla, 349, 384, 467
permanence of the chromosomes, 39 *et sqq.*, 226, 449
Petunia, 208, 217, 231, 233, 362
Phæophyceæ, 6, 425
Phanæus, 94
Phaseolus, 42
phenotype, 11, 448
Philosamia cynthia, 56
  polyploid nuclei, 62
Phleum, 173, 176, 217, 218
Photinus, 389
Phragmatobia fuliginosa, 55, 56
  contraction of chromosomes, 53, 347

Phragmatobia fuliginosa—contd.
  fragmentation heterozygote, 134
  lagging of chromosomes, 111
  sex chromosomes, 379
Phrynotettix magnus
  differential precocity, 290
  karyomeres, 45, 91
  pachytene, 94
  spiral structure, 32
  unequal bivalents, 153, 274 *et sqq.*
Phycomycetes, 2, 6, 15
Phylloxera, 346, 431
Physaloptera, 111
Pisum sativum
  anaphase, 112
  chiasmata, 109, 258
  crossing-over, 267, 409
  figure-of-eight, 409
  interchange, 142, 408
  interlocking, 273
  terminalisation, 320 *et sqq.*
  translocation, 481
Plantago, 211
plastids, 2
Platypœcilus, 397
Poa, 423
Pogonatum, 386
Poisson curve, 95
(G) polar bodies, 7, 10, 87, 439;
  granule, 35, 265
    v. attachment.
polarisation, 92, 158
Polemonium, 109, 150
pollen grain, 7, 179, 235, 236
  in fertilisation, 425 *et sqq.*
  in haploids, 365
  of *Œnothera*, 400
  polymitosis in, 367
  size, 179, 205
  viability, 230 *et sqq.*
pollen tube, 3, 8, 25
polymitosis, 366, 452, 456
(G) polyploids
  failure of pairing, 356
  hybrids between, 185
  size of, 206
polyploidy, 59
  after regeneration, 429
  in animals, 65
  and apomixis, 444
  classification, 169 *et sqq.*
  in evolution, 476, 484
  high polyploidy, 180, 203
polyploidy induced, 62
  inference of, 65, 77, 212, 221 *et sqq.*
  interchange heterozygotes, 146
  origin of, 61, 173, 181, 219
  polyploid species, 181
  secondary polyploidy, 59, 223, 239, 481
  segregation, 248
  within species, 211, 446, 480, 481
(G) polysomy, 59, 66
  v. secondary polyploid, tetrasomic and trisomic.
Pomoideæ, 81, 224 *et sqq.*, 481
Populus, 164, 386
Portulaca, 210
Potentilla, 211, 434, 442 *et sqq.*, 470
(G) precocity
  differential, 345, 396 *et sqq.*
  failure of, 343 *et sqq.*
  of mitosis, 302 *et sqq.*
  theory, 306
Primula
  chromosome complements, 82
  species, 481
  kewensis
    chromosome pairing, 162, 170 *et sqq.*, 182
    segregation, 247
    theory of doubling, 489
    unbalanced forms, 60, 237
  malacoides, 201
  obconica, 201, 208
  Sieboldii, 120, 200
  sinensis, 109, 116 *et sqq.*, 171, 178, 251, 265, 277, 340
Pristiurus, 94, 100, 108
(G) pro-chromosomes
(G) prophase
  meiosis, 88 *et sqq.*, 114 *et sqq.*
  mitosis, 19 *et sqq.*
proportion (of genes), 244 *et sqq.*, 478
  v. balance, and structural change.
Protenor, 379
(G) prothallia, 6, 419
Protista, 2 *et sqq.*, 18, 28 *et sqq.*, 458
(G) protoplasm, 1
Protortonia, 372 *et sqq.*
Prunus
  autosyndesis, 185

- *Prunus—contd.*
  - chromosome complement, 82
  - diakinesis, 314
  - failure of pairing, 356
  - hybrids, 162
  - multivalents, 123, 179, 340
  - polyploid species, 197, 198, 200, 212
  - syndiploidy, 63
  - triploids, 194, 200
  - unreduced gametes, 359
  - *laurocerasus*, 85, 180, 203
- *Pseudococcus*, 372 *et sqq.*
- pseudogamy, 369, 428, 441
- Pteridophyta, 6, 8, 419
- *Pteronidea*, 418
- *Pygæra*
  - failure of pairing, 353
    - reduction, 359
  - hybrids, 163
  - segregation, 247
  - triploids, 66, 177, 192
  - zygotene, 92
- *Pyrus Malus*
  - autosyndesis, 185
  - constitution, 197
  - multivalents, 123
  - progeny of triploids, 239
  - second division, 126
  - secondary pairing, 222 ; polyploidy, 223 *et sqq.*, 239
  - syndiploidy, 64
  - triploid, 194

- (G) QUADRIVALENTS, 63, 118, 172, 184 *et sqq.*, 310
  - *v.* rings.
- quantitative methods, 487

- *RANA esculenta*, 13, 109, 397, 442, 466
  - chiasmata, 108
  - chromosome form, 37
  - fragments, 70, 73, 75
  - separation of bivalents, 111
  - tetraploid, 211
  - triploid, 199
  - *Ficaria*, 211
- *Raphano-Brassica*
  - cell size, 205 *et sqq.*
  - failure of reduction, 357
  - pairing, 163
  - syndiploidy, 63
  - tetraploidy, 170 *et sqq.*
- rat, 53
- (G) reduction
  - failure of, 64, 167, 173, 358 *et sqq.*, 412 *et sqq.*, 431, 471
  - inference of, 87
  - of unequal bivalents, 273 *et sqq.*
  - zygotic and gametic, 5, 6
- (G) reductional split, 252 *et sqq.*
- reduplication, 67, 135, 139, 147, 235 *et sqq.*, 261, 481
- regeneration, 65, 429 *et sqq.*
- Renner effect, 400, 423
- reproduction
  - apomictic, 416 *et sqq.*
  - asexual, 4
  - semi-clonal, 371
  - sexual, 4 *et sqq.*, 456 *et sqq.*
- resting nucleus, 16 *et sqq.*, 42 *et sqq.*, 486
- resting stage
  - before meiosis, 91
  - in mitosis, 45, 219
  - during prophase, 94
- (G) restitution nucleus, 358, 431, 435 *et sqq.*
- *Rhabditis*, 23, 349, 431 *et sqq.*, 441 *et sqq.*, 469
- Rhizopoda, 6
- *Rhodites*, 431
- Rhodophyceæ, 6
- *Rhœo discolor*
  - chromosome form, 37, 83
  - deficient gametes, 231
  - pairing, 142, 144
  - ring-formation, 475
  - as a species, 482
  - stability, 482
  - terminal chiasmata, 105, 109
- *Rhogostoma schüsteri*, 27
- *Ribes*, 37, 46, 82, 153, 163, 352, 359, 489
- (G) ring chromosomes
  - at meiosis, 132, 296 *et sqq.*, 402 *et sqq.*, 460, 475
  - at mitosis, 38, 39 (Fig. 5)
  - segregation, 248, 339
- *Rosa*
  - interchange, 148, 150
  - interlocking, 273
  - multiple chiasmata, 117
  - precocity, 350
  - proof of crossing-over, 265, 267
  - pseudogamy, 442
  - reduplication, 147

Rosa—contd.
  terminalisation, 105, 314 *et sqq.*, 321 *et sqq.*
  acicularis, 211
  canina, 359, 368 *et sqq.*
  Caninæ, 208
  Cinnamomeæ, 208
Rosaceæ, 224
Rotifera, 418, 431
Roux, W., 19, 302
Rubus, 175 *et sqq.*, 190, 197, 217, 222, 442
Rumex
  bouquet stage, 92
  Acetosa, 183, 199, 381, 386, 390, 393
  Acetosella, 109, 152, 197, 385
  Hydrolapathum, 180, 209

SACCHARUM, 177, 346, 359, 362
Salamandra maculosa, 37, 273
Salix, 163, 177, 192, 203, 211, 226, 362, 386
Saprolegnia mixta, 85, 424, 438
satellite. *v.* trabant.
Saturnia, 163, 177, 192
Saxifraga, 174
Schistocerca pudibunda, 84
Schizophyllum, 424, 438
Sciara, 375, 394
scientific method, ix, 343, 450, 486 *et sqq.*
  v. technique.
Scilla, 355, 363
Scolopendra, 100
Scolopendrium, 419, 429
sea-urchin. *v.* echinoderm.
Secale, 32, 59, 135, 191, 354
second division, 91, 114, 126, 304, 459
sectioning, 491
(G) segment, 140, 298, 404
segmental interchange. *v.* interchange.
segmentation of egg, 45 ; spireme, 294
(G) segregation, 227, 247, 398 *et sqq.*
(G)   secondary, 188, 209, 476
  with non-reduction, 471
(G) semi-heterotypic division
semi-sterile, 143
set. *v.* chromosome.
sex chromosomes
  at anaphase, 361
  evolution of, 393–8, 460 *et sqq.*
  identification, 378, 386
  non-disjunction, 389
  pairing, 333, 387
  precocity, 348 *et sqq.*
  segregation, 248, 388
sex determination, 13, 372, 390, 464
sexual differentiation, 461
sexual reproduction, 4
  origin, 455, 483
Silene, 82, 210, 386
smears, 32, 491
Smerinthus, 163, 353
Solanum
  pollen grains, 179, 204
  triploid, 194
  Lycopersicum
    chromosome form, 38
    fragments, 135, 242
    haploid, 365
    induced polyploidy, 62
    progeny of triploid, 233
    tetraploid, 120, 171, 178, 200
    triploid, 120, 200
    unbalance, 238
  nigrum, 212
    haploid, 184, 425
    hybrid, 174
    tetraploid, 170, 178
Solenobia, 70, 432, 444, 446
Sorbus, 162
Sorghum, 219
Spartina, 217
species
  hybrids between, 128, 150, 162
  nature of, 480
  in *Œnothera*, 398 *et sqq.*
  polyploid, 196
  polyploidy within, 209
(G) sperm, spermatozoid, spermatozoon, 7 *et sqq.*
(G)   apyrene, oligopyrene, 9
  middle-piece, 22
(G) spermatocyte, spermatogenesis, 7, 91, 94
(G) spermatogonial cell
Sphærocarpus Donnellii, 14, 53, 248, 379, 440
Sphæromyxa sabrazesi, 36, 85
Spilosoma lubricipeda, 81
Spinacea oleracea, 111, 219

spindle, 22 *et sqq.*, 103, 104
  abnormalities, 64, 341
  failure of, 357, 359
  relation to univalents, 165
    v. chromosome movement.
spindle attachment, 25, 35, 48, 49, 98, 104, 113, 114, 143, 168, 220
  and complexes, 407
  and crossing-over, 283, 290
  division, 300, 303 *et sqq.*, 337, 366, 455
  origin, 452
  and reduction, 274 *et sqq.*
  repulsion between, 300, 303, 326 *et sqq.*, 340, 411, 459
  and spiralisation, 290
  and terminalisation, 314 *et sqq.*, 459
spindle-fibres, 24
spindle mechanism
  abnormal, 373
  development of, 453, 458
spindle-poles, 338
spiral structure, 30 *et sqq.*, 487 *et sqq.*
  and contraction, 291
  in crossing-over, 290 *et sqq.*
  at interphase, 113
(G) spireme, 21, 294
  continuous, 294, 403
Spirochona, 29
Spirogyra, 438
Spironema fragrans, 83
Spirostomum, 29
(G) spore, 6, 416 *et sqq.*
(G) sporophyte, 6, 419
Sporozoa, 6
staining, 488, 491
Stenobothrus
  anaphase, 270
  bouquet stage, 92
  chiasma-frequency, 286
  chiasmata, 108
  condensation, 350
  fusion, 80
  interlocking, 273
  meiosis, 96
  mitotic chromosomes, 36
  spermatogenesis, 8
  spindle, 26, 27
  spiral structure, 32
  terminalisation, 314, 323
  translocation, 71
  unequal bivalents, 153
sterility, 143, 172, 178, 423, 480
  v. fertility.
(G) strepsitene
structural change, 47 *et sqq.*, 67 *et sqq.*, 159, 209, 223, 228, 241, 245, 450, 454 *et sqq.*
  primary and secondary, 243, 250, 260
  in sex chromosomes, 380, 396
structural hybrid, 67, 130, 132 *et sqq.*
  in *Œnothera*, 404
  in sex-heterozygotes, 380 *et sqq.*
  terminalisation in, 320
(G) structure of chromosomes, 67, 130
(G) synapsis. *v.* contraction, pairing, synizesis and zygotene.
(G) syndiploidy, 63, 173, 359, 365
(G) syngamy
(G) synizesis, 92, 295, 487
Syrbula acuticornis, 286
Syringa, 64, 362
systematists, 128, 480, 482

TARAXACUM, 420 *et sqq.*, 431 *et sqq.*, 443, 445
Taxus baccata, 108
technique, 486, 491
(G) telomitic
(G) telophase
  meiosis, 90, 91
  mitosis, 27
    v. interphase mitosis, 27
(G) telosynapsis, 294, 487
Tenodera, 381, 385
Tephrosia, 444
(G) terminal affinity
(G) terminalisation, 103, 116, 310 *et sqq.*
  arrest of, 258, 319
  coefficient, 311
  in fragments, 136
  and interlocking, 271
  origin of, 459
  and telosynapsis, 295
(G) tetrad, 365, 367
Tetranychus, 418
tetraploid. *v.* polyploid.
tetraploid nuclei, 62
(G) tetrasomic, 60, 147, 233
Tettigidæ, 100, 277
Tettigonia, 32, 108, 349
Thalictrum, 42, 434
Thallophyta, 424

Thismia, 420, 432
Thyanta, 379
Thysanoptera, 465
time co-ordination, 307, 345, 366, 451, 455, 459 *et sqq.*
tissue culture, 3
(G) trabants, 35, 38, 39
  loss of, 55
Tradescantia, 17, 18, 26, 27
  bouquet stage, 92
  branched chromosome, 38
  cell size, 205
  chromosome permanence, 44
  division of fragments, 304
  fragments, 67, 69 *et sqq.*, 73, 135 *et sqq.*
  lateral chiasmata, 138
  multiple chiasmata, 117
  spiral structure, 32, 33
  terminalisation, 320
  translocation, 138
  triploid pollen grains, 231, 238
 bracteata, 147
 brevicaulis, 52
Tragopogon, 162
(G) translocation, 67 *et sqq.*
  heterozygotes, 138, 280
    in sex chromosomes, 385
    in species, 481
    reciprocal. *v.* interchange.
Trialeurodes, 418, 432
Trichoniscus, 199, 205, 446
Trimerotropis citrina, 143, 151, 267, 274, 338, 355
(G) triploids
  classification, 192, 199
  distribution of chromosomes, 126
  interchange heterozygotes, 147
  in the Liliaceæ, 66
  origin, 174, 412
  from polyploids, 184
  progeny of, 232
  segregation in, 231
Tripsacum, 190, 426
Trirhabda, 379
(G) trisomics
  fragments, 136
  interchange heterozygotes, 146
  origin of, 66, 411
  pairing in, 120
  progeny of, 232
  secondary, 139
  tertiary, 146
  types of, 236
Triticum
  autosyndesis, 184, 186, 190 *et sqq.*
  bivalents in hybrids, 160, 164, 165, 283
  cell size, 208
  interchange heterozygotes, 147, 152
  multiple chiasmata, 117
  origin of tetraploids, 171, 176
  terminalisation, 109, 158
 compactum, 63, 184, 197, 426
 durum, 356
 vulgare, 197
   failure of pairing, 353, 354, 356
   polyploidy, 217
   precocity, 346
   unbalanced forms, 237
(G) trivalents, 116 *et sqq.*
Tryxalis, 349
Tulipa
  chiasma frequency, 280, 283
  embryo-sac, 65, 422
  meiosis in, 88 *et sqq.*, 114 *et sqq.*
  spiral structure of chromosomes, 32
  terminalisation, 108, 313 *et sqq.*
  trivalents, 117, 265
 Clusiana, 198, 201, 202
 præcox, 199
 saxatilis, 199
 stellata, 197, 356
Turbellaria, 7

ULOTHRIX, 438
ultra-violet light, 486
(G) univalents (unpaired chromosomes)
  behaviour of, 165, 337, 341
  occurrence of.
    v. chromosomes.
Uvularia, 60, 69, 84, 108, 204, 231

VAHLKAMPFIA, 29
Valeriana, 211
Vallisneria, 208, 217
Vanduzea, 388
variation, 132, 245, 478, 481
Vaucheria, 425, 437, 443
vegetative propagation, 4
Veltheimia viridiflora, 37
Vespa, 418

viability, 230 *et sqq.*
Vicia, 32
  chiasmata, 98, 101, 283
  fragmentation, 57, 70
  hybrids, 53, 134, 153
  non-reduction, 363
  parthenogenesis, 426
  tetraploid, 212
  translocation, 138
  triploid, 200
de Vilmorin, H., 11
Viola
  failure of pairing, 353
  hybrids, 155, 163, 186, 191
  polyploids, 210, 225
  translocation heterozygote, 138
  Battaudieri, 203
  canina, 82, 203
  striata, 111
    polyploidy, 211
  tricolor × *Orphanidis*, 53
Vipera aspis, 84
virus, 452
Vitis, 339
vivipary, 4, 423, 445, 446
De Vries, H., 399

WEISMANN, A., 11, 40, 87

(G) X-CHROMOSOME, 68, 183, 384
  attached-X, 68, 70, 264, 279
  loss of, 361, 389, 440
    v. sex chromosomes.
X-raying
  Crepis, 70
  Datura, 69
  Drosophila, 71, 72, 75, 151, 409
  Nicotiana, 67
  Zea, 231
    v. Irradiation.

Y-CHROMOSOME, 463
  v. sex chromosomes.
Y^1-chromosome (*Drosophila*), 68, 71, 261, 264
Yucca filamentosa, 36, 84
  flaccida, 84, 286

ZACINTHA, 86
Zea Mays
  asynaptic, 334, 351
  failure of spindle, 360
  fragmentation, 71, 135
  hybrid, 190
  interchange, 57, 142, 151
  linkage maps, 277
  monosomic, 230
  multinucleate cells, 63
  nucleoli, 18
  origin of tetraploid, 176
  polymitosis, 367
  polysomic, 60
  proof of crossing-over, 263
  spiral structure, 32
  terminalisation, 109, 321
  triploid, 120, 199
    progeny, 233
Zebrina pendula, 32, 83, 153
Zephyranthes, 421 *et sqq.*, 441
Zoogonus minus, 108
Zygopetalum, 423, 442
(G) zygote
  definition, 4 *et sqq.*
  hybridity, 129 *et sqq.*
(G) zygotene
  description, 88, 91, 114
  misinterpretation, 290

PRINTED IN GREAT BRITAIN BY THE WHITEFRIARS PRESS LTD.
LONDON AND TONBRIDGE.

No. 2.

J. & A. CHURCHILL

Selected Books for Students and Practitioners of Medicine.

LONDON
40, Gloucester Place,
Portman Square, W. 1.

INDEX.

PAGE
2 Anatomy. Physiology. Biochemistry.
3 Materia Medica. Pharmacy.
4 Hygiene. Bacteriology.
5 Pathology. Psychology. Electrotherapeutics. Dictionaries.
6 Medicine.
7 Medicine. Massage.
8 Surgery.
9 Surgery. Anæsthetics.
10 Dermatology. Neurology. Urinary Disorders. Tropical Diseases.
11 Midwifery. Gynæcology.
12 Medical Jurisprudence. Ophthalmology.
13 Otology. Pædiatrics. Dentistry.
14 Chemistry.
15 Chemistry. Physics.
16 Physics. Microscopy. Miscellaneous.

FREE ON . . . APPLICATION.

1. Complete Illustrated Catalogue.
2. Catalogue of Science Books.

Anatomy ✎ Physiology Biochemistry

Recent Advances in Anatomy. By H. Woollard, M.D. 4 Coloured Plates and 73 Text-figures. 12*s*. 6*d*. net.

Surgical Anatomy. By Grant Massie, F.R.C.S. 121 Illustrations, some in colour. 15*s*. net.

The Principles of Anatomy as Seen in the Hand. By F. Wood Jones, D.Sc., M.B., B.S., F.R.S. 125 Illustrations. 15*s*. net.

The Anatomy of the Human Skeleton. By J. Ernest Frazer, F.R.C.S. 2nd Edition. 219 Illus., many in colours. 28*s*. net.

Synopsis of Anatomy. By T. B. Johnston, M.B., Professor of Anatomy, Univ. of London. 2nd Ed. 11 Illus. 12*s*. 6*d*. net.

A Manual of Practical Anatomy. By the late Prof. A. W. Hughes, M.B. Edited by Arthur Keith, M.D. In three parts. Part I, 12*s*. 6*d*. net. Part II, 10*s*. 6*d*. net. Part III, 12*s*. 6*d*. net.

Heath's Practical Anatomy: a Manual of Dissections. Edited by J. E. Lane, F.R.C.S. Ninth Edition. 15*s*. net.

Clinical Applied Anatomy. By Charles R. Box, M.D., and W. McAdam Eccles, M.S.Lond., F.R.C.S.Eng. 45 Plates 12*s*. 6*d*. net.

Essentials of Surface Anatomy. By C. R. Whittaker, F.R.C.S. Third Edition. 17 Plates. 7*s*. 6*d*. net.

Text-Book of Anatomy and Physiology for Nurses. By E. R. Bundy, M.D. Sixth Edition. 266 Illustrations. 12*s*. net.

Elementary Anatomy and Physiology for Nurses. By P. M. Lodge. 3*s*. 6*d*. net.

The Adrenals: their Physiology, Pathology and Diseases. By Max A. Goldzieher, M.D. 73 Illustrations. 30*s*. net.

Starling's Principles of Human Physiology. Fifth Edition. Edited by C. Lovatt Evans, D.Sc., F.R.C.P., F.R.S., Jodrell Professor of Physiology, University College, London. 543 Illus. 21*s*. net.

An Introduction to Biophysics. By D. Burns, D.Sc., Professor of Physiology, Univ. of Durham. 2nd Ed. 116 Illus. 25*s*. net.

Practical Physiology. By G. V. Anrep, M.D., D.Sc., and D. T. Harris, M.B., B.S. With Introduction by Prof. E. H. Starling, C.M.G., F.R.S. With 197 Illustrations. 10*s*. 6*d*. net.

Human Physiology. By F. R. Winton, M.D., University Lecturer in Physiology, Cambridge, and L. E. Bayliss, Ph.D., Assistant in the Dept. of Physiology and Biochemistry, University College, London. 227 Illustrations. 15*s*. net.

Recent Advances in Physiology. By C. Lovatt Evans, D.Sc.Lond., F.R.C.P., F.R.S., Jodrell Professor of Physiology, University College. Fourth Edition. 113 Illustrations. 12*s*. 6*d*. net.

Recent Advances in Biochemistry. By J. Pryde, Lecturer in Physiological Chemistry, Welsh National School of Medicine. Third Edition. 42 Illustrations. 12*s*. 6*d*. net.

A Text-Book of Biochemistry for Students of Medicine and Science. By A. T. Cameron, M.A., D.Sc., F.I.C., F.R.S.C., Professor of Biochemistry, University of Manitoba. Third Edition. 2 Plates and 13 Text-figures. 15*s*. net.

A Course in Practical Biochemistry. By Prof. A. T. Cameron and Frank White, A.R.T.C., Ph.D., Asst. Professor of Biochemistry, University of Manitoba. 4 Plates and 23 Figures. 8*s*. 6*d*. net.

Materia Medica ∅ Pharmacy

Recent Advances in Materia Medica (Sera, Vaccines, Hormones and Vitamins). By J. H. Burn, M.D., Director of the Pharmacological Laboratories, Pharmaceutical Society of Great Britain. 25 Illustrations. 12*s*. 6*d*. net.

Applied Pharmacology. By A. J. Clark, *M.C.*, M.D., F.R.C.P., Professor of Materia Medica, University of Edinburgh. Fourth Edition. With 72 Illustrations. 17*s*. net.

A Text-Book of Pharmacology and Therapeutics. By A. R. Cushny, M.A., M.D., F.R.S. Ninth Edition. 73 Illustrations. 25*s*. net.

Hale-White's Materia Medica, Pharmacy, Pharmacology and Therapeutics. Twentieth Edition. Revised by A. H. Douthwaite, M.D., F.R.C.P. 10*s*. 6*d*. net.

Synopsis of Pharmacology. By D. V. Cow, M.D. Second Edition. Revised by G. Norman Myers, M.D. With 15 Illustrations. 7*s*. 6*d*. net.

A Text-Book of Materia Medica for Students of Medicine. By C. R. Marshall, M.D. 127 Illustrations. 10*s*. 6*d*. net.

Southall's Organic Materia Medica. Revised by E. W. Mann, B.Sc. Eighth Edition. 12*s*. 6*d*. net.

A Text-Book of Materia Medica. By Henry G. Greenish, F.I.C., F.L.S., Professor of Pharmaceutics to the Pharmaceutical Society. Fifth Edition. 297 Illustrations. 25*s*. net. **The Microscopical Examination of Foods and Drugs.** Third Edition. 209 Illustrations. 18*s*. net. **An Anatomical Atlas of Vegetable Powders.** 138 Illustrations. 12*s*. 6*d*. net.

Practical Pharmacognosy. By T. E. Wallis, B.Sc., F.I.C. Second Edition. 105 Illustrations. 12*s*. 6*d*. net.

First Lines in Dispensing. By H. B. Stevens and C. E. L. Lucas, A.I.C., F.C.S. Third Edition. 95 Illustrations. 7*s*. 6*d*. net.

By E. W. Lucas, C.B.E., F.I.C., and H. B. Stevens, O.B.E., F.I.C.

The Book of Pharmacopœias and Unofficial Formularies. 7*s*. 6*d*. net.

Practical Pharmacy. Third Edition. 224 Illus. 27*s*. net.

The Book of Receipts: containing a Veterinary Materia Medica. A Pharmaceutical Formulary. A Photographic Formulary. A Synopsis of Practical Methods employed in the Examination of Urine, Milk, Potable Waters, Sputum, etc. Twelfth Edition. 10*s*. 6*d*. net.

The Book of Prescriptions, with an Index of Diseases and Remedies. Eleventh Edition. 10*s*. 6*d*. net.

Medical and Pharmaceutical Latin for Students of Pharmacy and Medicine. By R. R. Bennett. Third Edition. 10*s*. 6*d*. net.

A Companion to the British Pharmacopœia. By Sir Peter Wyatt Squire., F.L.S., F.C.S. Nineteenth Edition. 25*s*. net. **The Pharmacopœias of 31 London Hospitals.** Ninth Edition. 12*s*. 6*d*. net.

The Pharmaceutical Formulary. By Henry Beasley. Twelfth Edition by J. Oldham Braithwaite. 6*s*. 6*d*. net.

Favourite Prescriptions, Including Dosage Tables and Hints for Treatment of Poisoning. By Espine Ward, M.D., West African Medical Staff. Second Edition. Interleaved. 5*s*. net.

Hygiene ⁂ Bacteriology

The Health of the Industrial Worker. By E. L. Collis, M.D., Professor of Preventive Medicine, Welsh National School of Medicine, and Major Greenwood, M.R.C.P., M.R.C.S., Medical Officer, Ministry of Health. 30*s*. net.

The Principles of Preventive Medicine. By R. Tanner Hewlett, M.D., F.R.C.P., D.P.H., Professor of Bacteriology, University of London, and A. T. Nankivell, M.D., D.P.H., Medical Officer of Health, Hornsey. With 12 Charts and 5 Diagrams. 18*s*. net.

Synopsis of Hygiene. By W. Wilson Jameson, M.A., M.D., F.R.C.P., D.P.H., Professor of Public Health, London University, and Col. G. S. Parkinson, *D.S.O.*, M.R.C.S., L.R.C.P., D.P.H., Asst. Director, Public Health Division, London School of Hygiene and Tropical Medicine. Third Edition. 20 Illustrations. 18*s*. net.

A Simple Method of Water Analysis. By J. C. Thresh, M.D., D.P.H., and J. F. Beale, M.R.C.S., D.P.H. Tenth Edition. 3*s*. net.

Elementary Hygiene for Nurses. By H. C. Rutherford Darling, M.D., F.R.C.S. Fourth Edition. 54 Illustrations. 5*s*. net.

Preservatives in Food and Food Examination. By J. C. Thresh and Arthur E. Porter, M.D., M.A.Cantab. 8 Plates. 16*s*. net.

Foods and their Adulteration. By H. W. Wiley, M.D., Ph.D. Third Edition. 11 Coloured Plates and 87 Illustrations. 27*s*. net.
Beverages and their Adulteration. 42 Illustrations. 21*s*. net.

Text-book of Meat Hygiene. By R. Edelmann, Ph.D. Translated by J. R. Mohler, A.M., V.M.D., and A. Eichhorn, D.V.S. Fifth Edition. With 161 Illustrations and 5 Plates. 28*s*. net.

A Manual of Bacteriology, Clinical and Applied. By R. Tanner Hewlett, M.D., Professor of Bacteriology, University of London. Eighth Edition. 38 Plates and 63 Figures in the Text. 18*s*. net.

Immunity: Methods of Diagnosis and Therapy. By Dr. J. Citron. Second Edition. 40 Illustrations. 14*s*. net.

Clinical Diagnostic Bacteriology, including Serum- and Cyto-diagnosis. By A. C. Coles, M.D., D.Sc. 2 Plates. 8*s*. net.

The Chemical Analysis of Foods. By H. E. Cox, M.Sc. Ph.D., F.I.C. 38 Illustrations. 18*s*. net.

Medical Bacteriology, including Elementary Helminthology. By L. E. H. Whitby, *C.V.O.*, M.A., M.D., D.P.H., Assistant Pathologist, Middlesex Hospital. 75 Illustrations. 10*s*. 6*d*. net.

Recent Advances in Bacteriology. By J. H. Dible, M.B., Ch.B., Professor of Pathology, Univ. of Liverpool. Second Edition. 29 Illus. 15*s*. net.

Recent Advances in Preventive Medicine. By J. F. C. Haslam, *M.C.*, M.D., M.R.C.P., D.P.H., Director of Library Services, London School of Hygiene and Tropical Medicine. 30 Illustrations. 12*s*. 6*d*. net.

Dairy Bacteriology. By Dr. Orla-Jensen. Translated by P. S. Arup, B.Sc., F.I.C. Second Edition. 67 Illustrations. 18*s*. net.

Pathology ⌀ Psychology ⌀ Electro-therapeutics ⌀ Dictionaries

Laboratory Diagnosis; With Clinical Applications for Physicians. By E. E. Osgood, M.D., and H. D. Haskins, M.D., of the University of Oregon, U.S.A. 6 Coloured Plates and 21 Text-figures. 21*s*. net.

A Handbook of Clinical Chemical Pathology. By F. S. Fowweather, M.D., M.Sc., D.P.H., Lecturer in Chemical Pathology, Univ. of Leeds. With Foreword by Rt. Hon. Lord Moynihan, K.C.M.G. 18 Illus. 8*s*. 6*d*. net.

Pathology, General and Special, for Students of Medicine. By R. Tanner Hewlett, M.D., F.R.C.P., D.P.H., Professor of Bacteriology, University of London. 48 Plates and 12 Illustrations in Text. Fifth Edition. 18*s*. net.

Clinical Pathology. By P. N. Panton, M.B., Clinical Pathologist and Director of Hale Clinical Laboratory, London Hospital, and J. R. Marrack, M.B., Chemical Pathologist, London Hospital. Second Edition. With 12 Plates (10 Coloured) and 51 Illustrations in the Text. 15*s*. net.

A Manual of General or Experimental Pathology. By W. S. Lazarus-Barlow, M.D., F.R.C.P., Director of the Cancer Research Laboratories, Middlesex Hospital. Second Edition. 21*s*. net. **The Elements of Pathological Anatomy and Histology for Students.** 24*s*. net.

Surgical Pathology and Morbid Anatomy. See p. 8.

Post-Mortem Manual. By C. R. Box, M.D., Lecturer on Applied Anatomy, St. Thomas's Hospital. Second Edition. 22 Illustrations. 10*s*. 6*d*. net.

Recent Advances in Psychiatry. By H. Devine, O.B.E., M.D. 12*s*. 6*d*. net.

Psychological Medicine. By Sir M. Craig, C.B.E., M.D., Physician, Mental Diseases, Guy's Hospital, and T. Beaton, O.B.E., M.D., Lect. in Mental Diseases, Bethlem Royal Hospital. Fourth Edition. 25 Plates. 21*s*. net.

Recent Advances in Study of the Psychoneuroses. By Millais Culpin, M.D., F.R.C.S., Lecturer on Psychoneuroses, London Hospital Medical College. 12*s*. 6*d*. net.

Clinical Lectures on Psychological Medicine. By Henry Yellowlees, O.B.E., M.D., F.R.C.P. 12*s*. 6*d*. net.

The Journal of Mental Science. Published Quarterly, by Authority of the Royal Medico-Psychological Association. 7*s*. 6*d*. net.

Practical Electrotherapeutics and Diathermy. By G. B. Massey, M.D. 157 Illustrations. 21*s*. net.

Electro-Therapy: Its Rationale and Indications. By J. Curtis Webb, M.B., B.C. With 6 diagrams. 5*s*. net.

Electricity: Its Medical and Surgical Applications. By C. S. Potts, M.D. With 356 Illustrations and 6 Plates. 21*s*. net.

Lang's German-English Dictionary of Terms used in Medicine and the Allied Sciences. Fourth Edition, edited and revised by M. K. Meyers, M.D. *s*. net.

Medicine

Medical Emergencies. By Charles Newman, M.D., M.R.C.P., Junior Physician, King's College Hospital. 8*s.* 6*d.* net.

A Clinical Atlas of Blood Diseases. By A. Piney, M.D., M.R.C.P., and Stanley Wyard, M.D. 36 Illustrations, 32 Coloured. 12*s.* 6*d.* net.

Also by Dr. A. Piney

Recent Advances in Hæmatology. Third Edition. 4 Coloured Plates. 18 Text-figures. 12*s.* 6*d.* net.

Diseases of the Blood. 20 Illus., 6 in Col. 12*s.* 6*d.* net.

Skin: Its Uses in Six Phases. By Lewis E. Hertslet, M.R.C.S., L.R.C.P. With Forewords by Professor Leonard Hill, F.R.S., and R. P. Mackenzie, M.B., C.M., D.P.H. 8 Plates. 10s. 6d. net.

Taylor's Practice of Medicine. Fourteenth Edition. Revised by Drs. E. P. Poulton, C. P. Symonds, H. W. Barber and R. D. Gillespie. 64 Plates and 103 Figures. 25*s.* net.

Endocrine Diseases, Their Diagnosis and Treatment. By W. Falta (Vienna). Translated and Edited by M. K. Meyers, M.D. Foreword by Sir A. E. Garrod, M.D. 104 Illustrations. 36*s.* net.

Text-book of Differential Diagnosis of Internal Medicine. By M. Matthes. Translated from 4th German Edition by I. W. Held, M.D., and M. H. Gross, M.D. 176 Illustrations. 42*s.* net.

Medical Diagnosis. By A. Latham, M.D., F.R.C.P., and J. Torrens, M.B., M.R.C.P. 74 Illustrations, 19 in colour. 15*s.* net.

Pulmonary Tuberculosis. Its Diagnosis, Prevention, and Treatment. By W. M. Crofton, M.D. 21 Illustrations. 6*s.* net.
Therapeutic Immunisation: Theory and Practice. 7*s.* 6*d.* net.

Chill: Its Dangers and Prevention. By Marian Thornett, F.R.C.S.I. With a Foreword by Dr. Jane Walker, C.H. Illustrated. 3*s.* 6*d.* net.

Studies in Influenza and its Pulmonary Complications. By D. Barty King, O.B.E., M.D. 7*s.* 6*d.* net.

A Short Practice of Medicine. By R. A. Fleming, M.D., F.R.C.P.E., F.R.S.E., Lecturer on Medicine, School of Royal Colleges, Edinburgh. Third Edition. With 64 Illustrations. 21*s.* net.

The Blood: how to Examine and Diagnose its Diseases. By Alfred C. Coles, M.D., D.Sc., F.R.S.Edin. Third Edition. 7 Coloured Plates. 10*s.* 6*d.* net.

Lectures on Medicine to Nurses. By Herbert E. Cuff, M.D., F.R.C.S. Seventh Edition. 29 Illustrations. 7*s.* 6*d.* net.

On Alcoholism: Its Clinical Aspects and Treatment. By F. Hare, M.D., Med. Supt., Norwood Sanatorium, 5*s.* net.

Recent Advances in Cardiology. By C. F. Terence East, M.D., F.R.C.P., and C. W. C. Bain, M.C., M.B. Second Edition. 10 Plates and 62 Text-figures. 12*s.* 6*d.* net.

Recent Advances in the Study of Rheumatism. By F. J. Poynton, M.D., F.R.C.P., Physician, Univ. College Hospital, and B. E. Schlesinger, M.R.C.P., M.R.C.S., Physician, Children's Dept., Royal Northern Hospital. 25 Illus. 12*s.* 6*d.* net.

Medicine & Massage

Recent Advances in Allergy (Asthma, Hayfever, Eczema, Migraine, etc.). By G. W. Bray, M.B., B.Ch. 98 Illustrations. 12*s*. 6*d*. net.

Chemical Methods in Clinical Medicine. By G. A. Harrison, M.D., B.Ch., L.R.C.P., Reader in Chemical Pathology in the University of London. 2 Coloured Plates and 63 Text-figures. 18*s*. net.

Recent Advances in Medicine. Clinical—Laboratory—Therapeutic. By G. E. Beaumont, D.M., F.R.C.P., Assistant Physician, Middlesex Hospital, and E. C. Dodds, *M.V.O.*, M.D., B.Sc., Courtauld Professor of Biochemistry, Univ. of London. Sixth Edition. 51 Illus. 12*s*. 6*d*. net.

Recent Advances in Pulmonary Tuberculosis. By L. S. T. Burrell, M.D. Second Edition. 32 Plates and 17 Text-figures. 12*s*. 6*d*. net.

The Diabetic Life: Its Control by Diet and Insulin. By R. D. Lawrence, M.D., Chemical Pathologist, King's College Hospital. Sixth Edition. 14 Illustrations. 8*s*. 6*d*. net.

Massage: Its Principles and Practice. By James B. Mennell, M.A., M.D., B.C., Med. Officer, Physico-Therapeutic Dept., St. Thomas's Hospital. Second Edition. With 167 Illustrations. 21*s*. net.

Also by Dr. J. B. Mennell.

Backache. 48 Illustrations. 10*s*. 6*d*. net.

Translated and Edited by Dr. Mina L. Dobbie.

Medical Gymnastics and Massage in General Practice. By Dr. J. Arvedson. Third Edition. 8*s*. 6*d*. net.

The Technique, Effects and Uses of Swedish Medical Gymnastics and Massage. By J. Arvedson. Second Edition. 131 Illus. 12*s*. 6*d*. net.

Principles of Gymnastics for Women and Girls. By Elli Björkstén. 30 Illustrations. 8*s*. 6*d*. net.

Researches on Rheumatism. By F. J. Poynton, M.D., F.R.C.P., and A. Paine, M.D., B.S. 106 Illustrations 15*s*. net.

Physical Signs in the Chest and Abdomen. By A. J. Jex-Blake, M.D., F.R.C.P. 27 Illustrations. 9*s*. 6*d*. net.

Ulcer of the Stomach and Duodenum. By Samuel Fenwick, M.D., F.R.C.P., and W. Soltau Fenwick, M.D., B.S. 55 Illustrations. 10*s*. 6*d*. net. **Cancer and other Tumours of the Stomach.** 70 Illustrations. 10*s*. 6*d*. net.

Urine Examination made easy. By Thomas Carruthers, M.B., Ch.B. Fourth Edition. 2*s*. net.

Uric Acid as a Factor in the Causation of Disease. By Alexander Haig, M.D., F.R.C.P. Seventh Edition. 75 Illustrations. 14*s*. net. **Uric Acid in the Clinic.** 5*s*. net. **Uric Acid, an Epitome of the Subject.** Second Edition. 2*s*. 6*d*. net.

Medical Hydrology. By R. Fortescue Fox, M.D. 6*s*. net.

Physical Therapy in Diseases of the Eye, Ear, Nose and Throat. By A. R. Hollender, M.D., and M. H. Cottle, M.D. 21*s*. net.

Recent Advances in Chemotherapy. By G. M. Findlay, *O.B.E.*, D.Sc., Wellcome Bureau of Scientific Research. 4 Plates and 11 Text-figures. 15*s*. net.

Surgery

Science and Practice of Surgery. By W. H. C. Romanis, F.R.C.S., and P. H. Mitchiner, F.R.C.S. 2 vols. Third Edition. 716 Illustrations 28*s*. net.

By the same Authors.

Surgical Emergencies in Practice. 158 Illustrations. 18*s*. net.

Recent Advances in Radiology. By Peter Kerley, M.B., B.Ch., D.M.R.E., Assistant Radiologist, Westminster Hospital, London. 120 Illustrations. 12*s*. 6*d*. net.

Surgical Radiology. By A. P. Bertwistle, M.B., F.R.C.S.E. 24 Plates. 8*s*. 6*d*. net.

Surgery. Edited by G. E. Gask, C.M.G., D.S.O., F.R.C.S., and Harold W. Wilson, M.S., M.B., F.R.C.S., Surgeons, St. Bartholomew's Hospital. With 39 Plates, 20 in Colour, and 467 Text-figures. 30*s*. net.

The After-Treatment of Wounds and Injuries. By R. C. Elmslie, M.S., F.R.C.S., Special Mil. Surg. Hosp., Shepherd's Bush; Surgeon, St. Bartholomew's Hospital. With 144 Illustrations. 15*s*. net.

A Text-Book of Surgery. By R. Warren, M.D., F.R.C.S., Assistant Surgeon, London Hospital. With 504 Original Illustrations. 2 vols. 27*s*. net.

Bowlby and Andrewes' Surgical Pathology and Morbid Anatomy. Revised by Geoffrey Keynes, M.D., F.R.C.S., Assistant Surgeon, St. Bartholomew's Hospital. Eighth Edition. With 224 Illustrations. 21*s*. net.

On Diseases of the Rectum and Anus, including the Sixth Edition of the Jacksonian Prize Essay on Cancer. By Harrison Cripps, F.R.C.S., Surgical Staff, St. Bartholomew's Hospital. Fourth Edition. With 14 Plates and 34 Illustrations. 10*s*. 6*d*. net.

Diseases of the Rectum, Anus, and Sigmoid Colon. By F. Swinford Edwards, F.R.C.S., Senior Surgeon to St. Mark's Hospital for Fistula and other Diseases of the Rectum. Third Edition. 102 Illustrations. 10*s*. 6*d*. net.

Minor Surgery and Bandaging. Twentieth Edition. (Heath, Pollard and Davies). By Gwynne Williams, M.S., F.R.C.S., Surgeon, University College Hospital. 262 Illustrations. 10*s*. 6*d*. net.

Surgical Nursing and After-Treatment. By H. C. Rutherford Darling, M.D., F.R.C.S., Surgeon, South Coast Hospital, Sydney. Third Edition. With 149 Illustrations. 8*s*. 6*d*. net.

By the same Author.

Elementary Hygiene for Nurses. Fourth Edition. 54 Illustrations. 5*s*. net.

Surgery ✎ Anæsthetics

A Textbook of Surgical Pathology. By C. F. W. Illingworth, M.D., F.R.C.S.E., Clinical Tutor, Royal Infirmary, Edinburgh, and B. M. Dick, M.B., F.R.C.S.E., Clinical Tutor in Surgery, Royal Infirmary, Edinburgh. 290 Illustrations. *s. d.* net.

Radium Treatment of Cancer. By Stanford Cade, F.R.C.S., Assistant Surgeon and Joint Lecturer on Surgery, Westminster Hospital. With 13 Coloured Plates and 49 Text-figures. 15*s.* net.

The Operations of Surgery. Seventh Edition. By R. P. Rowlands, M.S.Lond., F.R.C.S., and Philip Turner, M.S., F.R.C.S., Surgeons, Guy's Hospital. 2 vols. 900 Illustrations, 43 in Colour. £3 10*s.* 0*d.* net.

Recent Advances in Surgery. By W. H. Ogilvie, M.D., F.R.C.S., Assistant Surgeon, Guy's Hospital. Second Edition. 115 Illustrations. 15*s.* net.

Surgery in the Tropics. By Sir Frank P. Connor, D.S.O., F.R.C.S., Professor of Surgery, Bengal Medical College. 99 Illustrations. 12*s.* 6*d.* net.

Surgery in War. By A. J. Hull, F.R.C.S., Lieut.-Col., R.A.M.C. With 210 Illustrations. 25*s.* net.

Operative Surgery of the Head, Neck, Thorax and Abdomen. By Edward H. Taylor, F.R.C.S.I., University Professor of Surgery, Trinity College, Dublin. With 300 Original Illustrations, many in colour. 32*s.* net.

Synopsis of Surgery. By Ivor Back, F.R.C.S., Surgeon, St. George's Hospital, and A. T. Edwards, F.R.C.S., Assistant Surgeon, Westminster Hospital. 12*s.* 6*d.* net.

Synopsis of Surgical Pathology. By Eric Pearce Gould, M.D., F.R.C.S. 6*s.* net.

Synopsis of Surgical Diagnosis. By W. H. C. Romanis, M.B., M.C., F.R.C.S. 8*s.* 6*d.* net.

Inguinal Hernia, the Imperfectly Descended Testicle, and Varicocele. By Philip Turner, M.S., F.R.C.S., Assistant Surgeon, Guy's Hospital. With 22 Illustrations. 10*s.* 6*d.* net.

Practice and Problem in Abdominal Surgery. By Alfred Ernest Maylard, M.B.Lond. and B.S. 39 Illustrations. 8*s.* 6*d.* net. **Abdominal Tuberculosis.** 57 Illustrations. 12*s.* 6*d.* net.

Clinical Essays and Lectures. By Howard Marsh, F.R.C.S. Prof. Surgery, Univ. Cambridge. 26 Figures. 7*s.* 6*d.* net.

Surgical Emergencies. By Paul Swain, F.R.C.S. Fifth Edition. 149 Engravings. 6*s.* net.

Chloroform: a Manual for Students and Practitioners. By Edward Lawrie, M.B.Edin. Illustrated. 7*s.* 6*d.* net.

Anæsthesia. By J. T. Gwathmey, M.D., President of the American Association of Anæsthetists, with Collaborators on Special Subjects. Second Edition. 273 Illustrations. 25*s.* net.

Dermatology ⌀ Urinary Disorders Neurology ⌀ Tropical Diseases

---

A Text-Book of Diseases of the Skin. By J. H. Sequeira, M.D., F.R.C.P., F.R.C.S., Physician, Skin Dept., London Hosp. 4th Edition. 56 Plates in colours and 309 Text-figures. 42*s*. net.

The Hair, its Care, Diseases and Treatment. By W. J. O'Donovan, *O.B.E.*, M.D., B.S., Physician, Skin Dept., London Hospital. 40 Illustrations. 12*s*. 6*d*. net.

Recent Advances in Neurology. By W. Russell Brain, M.D., Assistant Physician, London Hospital, and E. B. Strauss, B.M., B.Ch., Clinical Assistant, University of Marburg. Second Edition. 39 Illustrations. 12*s*. 6*d*. net.

A Text-Book of Nervous Diseases. By W. Aldren Turner, M.D., F.R.C.P., and T. Grainger Stewart, M.B., M.R.C.P. 188 Illustrations. 18*s*. net.

Diseases of the Kidney and Ureter. By W. Girling Ball, F.R.C.S., and Geoffrey Evans, M.D., F.R.C.P. 8 Colour Plates and 150 Illustrations. *s*. *d*. net.

Stone in the Urinary Tract. By H. P. Winsbury-White, M.B., Ch.B., F.R.C.S.Edin., F.R.C.S.Eng. 2 Coloured Plates and 181 Text-figures. 25*s*.

Selected Papers on Stone, Prostate, and other Urinary Disorders. By R. Harrison, F.R.C.S. 15 Illustrations. 5*s*. net.

By E. Hurry Fenwick, F.R.C.S., Surgeon to the London Hospital :

Atlas of Electric Cystoscopy. 34 Coloured Plates. 21*s*. net. **Obscure Diseases of the Urethra.** 63 Illus. 6*s*. 6*d*. net. **Tumours of the Urinary Bladder.** **Fasc. I.** 5*s*. net. **Ulceration of the Bladder, Simple, Tuberculous, and Malignant : a Clinical Study.** Illustrated. 5*s*. net.

The Nematode Parasites of Vertebrates. By Warrington Yorke, M.D., Professor of Parasitology, University of Liverpool, and P. A. Maplestone, M.B., D.S.O. Foreword by C. W. Stiles. 307 Illustrations. 36*s*. net.

Recent Advances in Tropical Medicine. By Sir Leonard Rogers, C.I.E., M.D., F.R.S., F.R.C.S., F.R.C.P. Second Edition. 16 Illustrations. 12*s*. 6*d*. net.

Malay Poisons and Charm Cures. By J. D. Gimlette, M.R.C.S., L.R.C.P. Third Edition. 3 Plates. 10*s*. 6*d*. net.

Public Health Practice in the Tropics. By J. Balfour Kirk, M.B., D.P.H., D.T.M.&H., Director, Medical and Health Department, Mauritius. 80 Illustrations. 15*s*. net.

Tropical Medicine. By Sir Leonard Rogers, C.I.E., F.R.C.P., F.R.C.S., F.R.S., and Major-General J. W. D. Megaw, I.M.S., C.I.E., M.B., B.Ch. 1 Colour Plate and 77 Illustrations. 14*s*. net.

Malarial Nephritis. By George Giglioli, M.D. (Italy), D.T.M.&H.(Eng.). 17 Illustrations. 8*s*. 6*d*. net.

Midwifery ⁂ Gynæcology

The Queen Charlotte's Practice of Obstetrics. By J. B. Banister, M.D., F.R.C.S., A. W. Bourne, M.B., F.R.C.S., T. B. Davies, M.D., F.R.C.S., C. S. Lane-Roberts, M.S., F.R.C.S., L. G. Phillips, M.S., F.R.C.S., L. C. Rivett, M.C., F.R.C.S., Members of the Staff of the Hospital. Second Edition. 274 Illustrations, 4 Coloured Plates. 18*s*. net.

Recent Advances in Obstetrics and Gynæcology. By Aleck W. Bourne, F.R.C.S., Obstetric Surgeon, St. Mary's Hospital. Second Edition. 67 Illustrations. 12*s*. 6*d*. net.

Practical Midwifery. By Gibbon FitzGibbon, M.D., F.R.C.P.I. With 175 Illustrations. 16*s*. net.

Handbook of Midwifery. By R. E. Tottenham, M.D., B.A.O., F.R.C.P.I., Professor of Obstetrics and Gynæcology, University of Hong-Kong. 102 Illustrations. 10*s*. 6*d*. net.

The Difficulties and Emergencies of Obstetric Practice. By Comyns Berkeley, M.D., F.R.C.P., and Victor Bonney, M.D., F.R.C.S. Third Edition. 309 Original Illustrations. 36*s*. net.

Manual of Midwifery. By T. W. Eden, M.D., C.M.Edin., F.R.C.P.Lond., and Eardley Holland, M.D., F.R.C.P., F.R.C.S., Obstetric and Gynæcological Surgeon, London Hospital. Seventh Edition. 9 Plates and 389 Text-figures. 21*s*. net.

Gynæcology. By T. W. Eden and C. Lockyer, M.D., F.R.C.P., F.R.C.S. Third Edition. 556 Illustrations and 32 Coloured Plates. 36*s*. net.

A Short Practice of Midwifery, embodying the Treatment adopted in the Rotunda Hospital, Dublin. By Henry Jellett, M.D., B.A.O.Dub., late Master, Rotunda Hospital, Dublin. Tenth Edition. 3 Coloured Plates and 283 Illustrations. 18*s*. net. **A Short Practice of Midwifery for Nurses,** with a Glossary of Medical Terms, and the Regulations of the C.M.B. Eighth Edition. 4 Coloured Plates and 176 Illustrations. 8*s*. 6*d*. net. **A Practice of Gynæcology.** Fifth Edition. 15 Col. Plates and 417 Illustrations (many coloured). 25*s*. net. **A Short Practice of Gynæcology.** Revised by Professor R. E. Tottenham, M.D., F.R.C.P.I. Sixth Edition. With 365 Illustrations. (many in colour). 21*s*. net. **The Causes and Prevention of Maternal Mortality.** 15*s*. net.

A Manual for Midwives. By J. B. Banister, M.D., F.R.C.S. Fourth Edition. 53 Illustrations. *s*. *d*. net.

Cæsarean Section. By Frances Ivens-Knowles, *O.B.E.*, M.B., M.S., Honorary Surgeon, Clapham Maternity Hospital, London. 5*s*. net.

By R. A. Gibbons, M.D., F.R.C.S.Ed.

A Lecture on Dysmenorrhœa. 2*s*. 6*d*. net. **A Lecture on Sterility: its Ætiology and Treatment.** 2*s*. 6*d*. net. **A Lecture on Pruritus Vulvæ: its Ætiology and Treatment.** 2*s*. 6*d*. net.

Practical Talks to Midwives. By E. M. Doubleday, S.R.N., Sister Tutor, Post Certificate School for Midwives, Camberwell. 17 Illustrations. 3*s*. 6*d*. net.

Medical Jurisprudence
Ophthalmology

Recent Advances in Forensic Medicine. By SYDNEY SMITH, M.D., D.P.H., Regius Professor of Forensic Medicine, University of Edinburgh, and J. GLAISTER, Jnr., M.D., Ch.B., Professor of Forensic Medicine, Cairo. 66 Illustrations. 12*s*. 6*d*. net.

An Introduction to Forensic Psychiatry in the Criminal Courts. By W. N. EAST, M.D. 16*s*. net.

Some Famous Medical Trials. By L. A. PARRY, M.D., F.R.C.S. 10*s*. 6*d*. net.

Forensic Medicine. By SYDNEY SMITH, M.D., D.P.H., Regius Professor of Forensic Medicine, University of Edinburgh. Third Edition. 170 Illustrations 24*s*. net.

Forensic Medicine. Illustrated by Photographs and Descriptive Cases. By H. LITTLEJOHN, F.R.C.S.Ed. 183 Illus. 15*s*. net.

Medical Jurisprudence: its Principles and Practice. By ALFRED S. TAYLOR, M.D. Eighth Edition, by SYDNEY SMITH, M.D., D.P.H., and W. G. H. COOK, LL.D., Barrister-at-Law. 2 vols. £3 3*s*. net.

Recent Advances in Ophthalmology. By W. STEWART DUKE-ELDER, M.D., F.R.C.S., Assistant Ophthalmic Surgeon, St. George's Hospital. Second Ed. 4 Coloured Plates and 110 Text-figs. 12*s*. 6*d*. net.

Also by Dr. Duke-Elder.

The Practice of Refraction. 208 Illus. 12*s*. 6*d*. net.

A Handbook of Ophthalmology. By HUMPHREY NEAME, F.R.C.S., and F. A. WILLIAMSON-NOBLE, F.R.C.S. 12 Coloured Plates. 194 Illustrations. 12*s*. 6*d*. net.

Refraction of the Eye, including Physiological Optics. By CHARLES GOULDEN, O.B.E., M.D., F.R.C.S., 180 Illustrations. 10*s*. 6*d*. net.

Medical Ophthalmology. By R. FOSTER MOORE, O.B.E., F.R.C.S. Second Edition. 92 Illustrations. 18s. net.

Refraction of the Eye. By G. HARTRIDGE, F.R.C.S. 16th Edition. 110 Illustrations. 7*s*. 6*d*. net. **The Ophthalmoscope.** 6th Edition. 65 Illustrations and 4 Plates. 6*s*. 6*d*. net.

Diseases of the Eye: a Manual for Students and Practitioners. By SIR J. H. PARSONS, *C.B.E.*, D.Sc., F.R.C.S., F.R.S., Ophthalmic Surgeon, University College Hospital; Sixth Edition. 348 Illustrations and 20 Coloured Plates. 18*s*. net. **Elementary Ophthalmic Optics, including Ophthalmoscopy and Retinoscopy.** 66 Illustrations. 6*s*. 6*d*. net.

Sight-Testing Made Easy, including Chapter on Retinoscopy. By W. W. HARDWICKE, M.D. Fourth Edition. 5*s*. net.

The Ophthalmoscope and How to Use It. By A. FREELAND FERGUS, LL.D., M.D., F.R.S.E. 2nd Edition. 17 Illus. 3*s*. 6*d*. net.

Principles of Ophthalmoscopy and Skiascopy. By G. F. ALEXANDER, M.B., C.M. 31 Illustrations. 5*s*. net.

Ophthalmological Society of the United Kingdom. Transactions. Annually. 30*s*. net.

The Slit-Lamp Microscopy of the Living Eye. By F. ED. KOBY. Translated by C. B. GOULDEN, O.B.E., M.D., F.R.C.S., and CLARA L. HARRIS, M.B., Ch.B. Second Edition. 104 Illus. 15*s*. net.

Ophthalmic Nursing. By M. H. WHITING, F.R.C.S. 51 Illustrations. 5*s*. net.

Otology ⌀ Pædiatrics ⌀ Dentistry

The Labyrinth of Animals, including Mammals, Birds, Reptiles, and Amphibians. By Albert A. Gray, M.D.(Glas.), F.R.S.E., Surgeon for Diseases of the Ear to the Victoria Infirmary, Glasgow. Vol. I, with 31 Stereoscopic Plates. 21*s*. net (including Stereoscope). Vol. II. 45 Stereoscopic Plates. 25*s*. net.

Manual of Diseases of Nose and Throat. By C. G. Coakley, M.D. Seventh Edition. 153 Illus. and 7 Coloured Plates. 18*s*. net.

The Pharmacopœia of the Hospital for Diseases of the Throat, Nose, and Ear. Seventh Edition. 2*s*. 6*d*. net.

Diseases of the Ear. By T. Mark Hovell, Senior Aural Surgeon to the London Hospital. 2nd Edition. 128 Engravings. 21*s*. net.

Recent Advances in Diseases of Children. By W. J Pearson, D.S.O., D.M., F.R.C.P., Physician, Children's Dept. University College Hospital, and W. G. Wyllie, M.D., M.R.C.P., Physician, Hospital for Sick Children, Gt. Ormond Street. Second Edition. 20 Plates and 34 Text-figures. 15*s*. net.

The Modern Practice of Pediatrics. By William Palmer Lucas, M.D., LL.D., Professor of Pediatrics, University of California Medical School. 126 Illustrations. 30*s*. net.

Premature and Congenitally Diseased Infants. By Julius H. Hess, M.D. With 189 Illustrations. 18*s*. net.

The Diseases of Children. By Sir J. F. Goodhart, Bt., M.D., F.R.C.P., and G. F. Still, M.D., F.R.C.P., Professor of the Diseases of Children, King's College. Twelfth Edition. 68 Illustrations. 28*s*. net.

An Introduction to Dental Anatomy and Physiology, Descriptive and Applied. By A. Hopewell-Smith, L.D.S.Eng. With 6 Plates and 340 Illustrations 21*s*. net. **The Normal and Pathological Histology of the Mouth.** Vol. I, Normal Histology. Vol. II, Pathological Histology. With 658 Illustrations. 2 vols. £2 2*s*. per set.

Dental Anatomy, Human and Comparative: a Manual. By Charles S. Tomes, M.A., F.R.S. Edited by H. W. Marett Tims, O.B.E., M.A., M.D., F.Z.S., and C. Bowdler Henry, L.R.C.P., M.R.C.S., L.D.S.Eng. Eighth Edition. 325 Illustrations. 18*s*. net.

A System of Dental Surgery. By Sir John Tomes, F.R.S. Revised by C. S. Tomes, M.A., F.R.S., and Walter S. Nowell, M.A.Oxon. Fifth Edition. 318 Engravings. 15*s*. net.

An Atlas of Dental Extractions, with Notes on the Causes and Relief of Dental Pain. By C. Edward Wallis, M.R.C.S., L.R.C.P., L.D.S. Second Edition. With 11 Plates. 6*s*. net.

A Manual on Dental Metallurgy. By Ernest A. Smith, Assay Office, Sheffield. Fourth Edition. 37 Illustrations. 12*s*. 6*d*. net.

Synopsis of Dentistry. By A. B. G. Underwood, B.S., L.D.S.Eng. With 10 Illustrations. 9*s*. 6*d*. net.

Handbook of Mechanical Dentistry. By J. L. Dudley Buxton, L.D.S., Dental Surgeon, University College Hospital. With 168 Illustrations. 12*s*. 6*d*. net.

Operative Dentistry. By W. H. O. McGehee, M.D., D.D.S., Head of the Dept. of Operative Dentistry, New York University College of Dentistry. 1040 Illustrations. 42*s*. net.

Physics
Microscopy ⌀ Miscellaneous

Recent Advances in Physics (Except Atomic). By F. H. Newman, D.Sc., Professor of Physics, Univ. Coll. of South-West England, Exeter. 51 Illustrations. 15*s.* net.

The Physics of X-Ray Therapy. By W. V. Mayneord, M.Sc., Physicist to Radio-Therapeutic Dept. of Cancer Hospital (Free), London. 106 Illustrations. 10*s.* 6*d.* net.

Elementary Physics. By G. Stead, M.A., Lect. in Physics, Univ. of Cambridge. Third Edition. 291 Illustrations. 10*s.* 6*d.* net.

A Handbook of Physics and Chemistry. By H. E. Corbin, B.Sc.Lond., and A. M. Stewart, B.Sc.Lond. Fifth Edition. 200 Illustrations. 12*s.* 6*d.* net.

A Treatise on Physics. By Andrew Gray, LL.D., F.R.S. Vol. I. Dynamics and Properties of Matter. 350 Illus. 18*s.* net.

The Principles of Radiography. By J. A. Crowther, Sc.D., F.Inst.P. With 55 Illustrations. 7*s.* 6*d.* net.

Recent Advances in Microscopy. Edited by A. Piney, M.D., M.R.C.P., Director, Pathological Department, Cancer Hospital, London. Illustrated. 12*s.* 6*d.* net.

Elementary Histological Technique for Animal and Plant Tissues. By J. T. Holder, F.R.M.S. 23 Illustrations. 7*s.* 6*d.* net.

The Microtomist's Vade-Mecum. By Arthur Bolles Lee. Ninth Edition Edited by J. Brontë Gatenby, D.Sc. 30*s.* net.

Plant Anatomy. By William Chase Stevens, Prof. of Botany in the Univ. of Kansas. Fourth Edition. 155 Illustrations. 21*s.* net.

A Text-book of Mycology and Plant Pathology. By J. W. Harshberger. With 271 Illustrations. 24*s.* net.

A Text-Book of Botany, for Medical and Pharmaceutical Students. By J. Small, D.Sc., F.L.S., Professor of Botany, Queen's University, Belfast. Second Edition. 1350 Illustrations. 21*s.* net.

Also by Prof. J. Small

Practical Botany. 35 Illustrations. 10*s.* 6*d.* net.
Pocket Lens Plant Lore. 25 Illustrations. 5*s.* net.

Recent Advances in Plant Physiology. By E. C. Barton-Wright, M.Sc., Lecturer in Botany in the University of London. 51 Illustrations. 12*s.* 6*d.* net.

Also by E. C. Barton-Wright.

Recent Advances in Botany. Illustrations. 15*s.* net.

Recent Advances in Entomology, By A. D. Imms, D.Sc., F.R.S., Chief Entomologist, Rothamsted Experimental Station, Harpenden. 84 Illustrations. 12*s.* 6*d.* net.

The Mothercraft Manual. By M. Liddiard, S.R.N., Matron Mothercraft Training Society. Eighth Edition. 36 Illustrations. 3*s.* 6*d.* net.

J. & A. CHURCHILL
40, GLOUCESTER PLACE, PORTMAN SQUARE, W. 1.

279825 Biol
D

Author Darlington, C.D.

Title Recent advances in cytology.

University of Toronto
Library

DO NOT
REMOVE
THE
CARD
FROM
THIS
POCKET

Acme Library Card Pocket
LOWE-MARTIN CO. LIMITED